Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s)

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ABSTRACT

Savenkoff, C., H. Bourdages, M. Castonguay, L. Morissette, D. Chabot, and M. O. Hammill. 2004. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2531: vi+93 pp.

Mass-balance models were used to reconstruct trophic flows through the whole northern Gulf of St. Lawrence ecosystem (NAFO divisions 4RS) for the mid-1990s period, after the groundfish stock collapses. The whole-system model of the northern Gulf of St. Lawrence is divided into 32 functional groups or compartments from phytoplankton and detritus to marine mammals and seabirds, including harvested species of pelagic, demersal, and benthic domains. We present here details of the input data (biomass, production, consumption, export, and diet composition) for each compartment used for modelling. The successful development of ecosystem models proposed by the Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic (CDEENA) program will provide powerful new tools to evaluate the impact of human and environmental factors on a variety of Atlantic shelf ecosystems.

RÉSUMÉ

Savenkoff, C., H. Bourdages, M. Castonguay, L. Morissette, D. Chabot, and M. O. Hammill. 2004. Input data and parameter estimates for ecosystem models of the northern Gulf of St. Lawrence (mid-1990s). Can. Tech. Rep. Fish. Aquat. Sci. 2531: vi+93 pp.

Des modèles d'équilibre de masse ont été utilisés pour représenter les flux trophiques de l'écosystème complet du nord du Golfe du Saint-Laurent (divisions 4RS de l'OPANO) pour le milieu des années 1990, après l'effondrement des stocks de poissons de fond. L'écosystème du nord du Golfe du Saint-Laurent a été divisé en 32 groupes ou compartiments trophiques depuis le phytoplancton et les détritus jusqu'aux oiseaux et mammifères marins incluant les espèces commerciales des domaines pélagique, démersal et benthique. Nous présentons ici le détail des données (biomasse, production, consommation, export et composition alimentaire) pour chaque groupe utilisé pour les modélisations. Le succès de l'élaboration des modèles écosystémiques proposés par le programme « Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic » (CDEENA) apportera de nouveaux outils scientifiques puissants pour évaluer l'impact des facteurs humains et environnementaux dans différents écosystèmes côtiers de l'Atlantique.

PREFACE

This work was supported by a multidisciplinary and inter-regional program known as CDEENA (Comparative Dynamics of Exploited Ecosystems in the Northwest Atlantic). CDEENA originally proposed a comparative analysis of changes in the structure and function of northwest Atlantic shelf ecosystems to determine how these may have affected the productivity of living resources. To this end, CDEENA brought together the expertise of field scientists and modellers to: (1) describe the changes in time and space, (2) identify and fill critical data gaps in the knowledge base, and (3) develop models to investigate ecosystem-level hypotheses (i.e., environmental variation, predation, fishing effects) concerning changes in reproduction, mortality, growth, and feeding of cod and other species.

The ecosystems that have been studied are the Newfoundland Shelf (NAFO 2J3KLNO), the northern Gulf of St. Lawrence (NAFO 4RS), the southern Gulf of St. Lawrence (NAFO 4T), and the eastern Scotian Shelf (NAFO 4VsW). CDEENA focused on two periods: (1) the mid-1980s, prior to the groundfish collapses of the early 1990s in virtually all areas, and (2) the mid-1990s, when the collapsed groundfish stocks failed to recover following fishery closures in most areas. The program tested the hypothesis that the failure of the collapsed fish stocks to recover in the 1990s was explained by changes in the ecosystems of the NW Atlantic (e.g., changes in trophic structure) driven by a combination of biological, fishing, and environmental variation.

INTRODUCTION

In the early 1990s, abundance of many Northwest Atlantic cod populations (*Gadus morhua* L.) declined to low levels resulting in cessation of directed fishing for these stocks. More than a decade later, in spite of limited fishing, almost all of these stocks show no signs of recovery and abundance continues to decline in some cases (Rice and Rivard 2003). The collapse of the cod fishery was generally attributed to a combination of intense exploitation and environmental changes that led to a reduction in recruitment and an increase in natural mortality (Dutil et al. 1998). Like other Atlantic cod stocks, the northern Gulf of St. Lawrence stock shows limited signs of recovery (Fréchet et al. 2003), which led to a second moratorium in April 2003. Traditional studies on Atlantic cod stocks have followed a single species approach, where abundance was evaluated using virtual population analysis incorporating catch data from the commercial fishery and research vessel surveys. However, the single-species approach ignores the effects of external factors such as prey abundance, predation, or competition from other components of the ecosystem. Owing to the widespread nature of the Atlantic cod collapse and its failure to recover, it is evident that a larger all-encompassing approach is needed to understand whether all of the cod stocks are affected in a similar way. Consequently, the Department of Fisheries and Oceans developed a multi-year research program entitled Comparative Dynamics of Exploited Ecosystems of the Northwest Atlantic (CDEENA) to examine changes that might have occurred in the northwest Atlantic ecosystems over the last 15 years. The objective was to develop individual ecosystem models for the northern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization [NAFO] divisions 4RS), the southern Gulf of St. Lawrence (NAFO division 4T), the Newfoundland and Labrador coast and offshore region (NAFO divisions 2J3KLNO), and the eastern Scotian Shelf region off the coast of Nova Scotia (NAFO divisions 4VsW). Different models were thus constructed at two specific periods: (1) the mid-1980s, which represents the period before the collapse of groundfish stocks in the early 1990s, and (2) the mid-1990s, when the collapsed groundfish stocks had failed to recover.

Here we present the data and input parameters used to construct inverse and Ecopath models of the northern Gulf of St. Lawrence ecosystem (NAFO divisions 4RS; Figure 1) during the post-collapse (1994–1996) period. The inverse model was useful to obtain a first balanced solution using an objective least-squares criterion. Throughout the modelling process, different approaches (comparisons of different flow networks, random perturbations, sensitivity tests, etc.) were applied to assess the solution's robustness to variations in the data as well as to provide an overall view of the ecosystem, to identify robust patterns, and to determine the location of uncertainties in the food web. The final solution obtained was the mean of 31 balanced random perturbations (including a response without perturbation). An Ecopath model was then constructed using this final solution to estimate important ecological indices (e.g., mean trophic level of the catches, trophic levels assigned to individual compartments, connectance, and omnivory). The Ecopath solution was also used in dynamic simulations between time periods using Ecosim software (Christensen et al. 2000). The estimates from inverse modelling were also shown for comparisons.

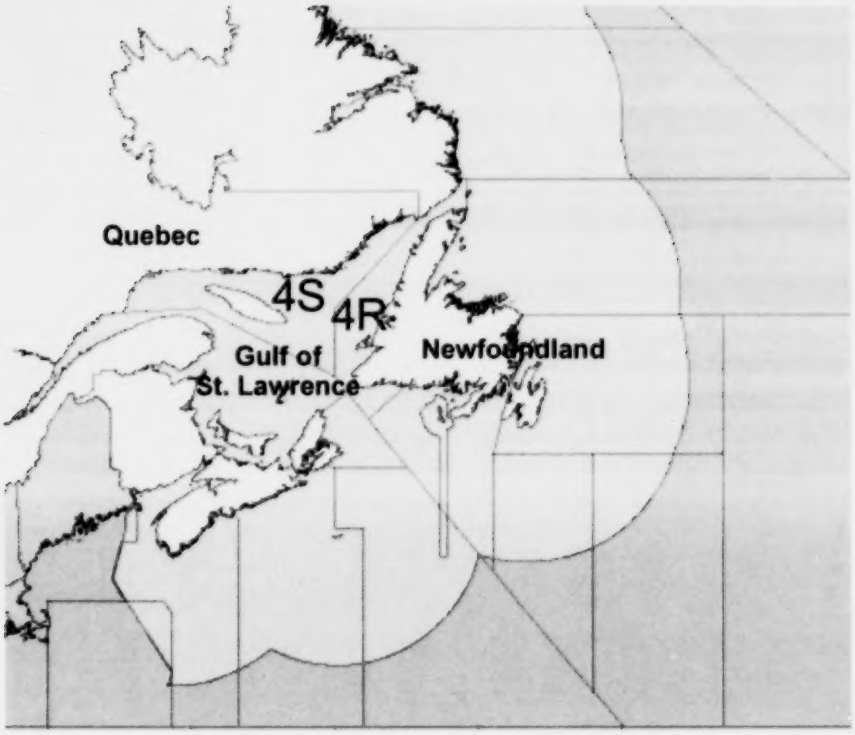

Figure 1. Northern Gulf of St. Lawrence (NAFO divisions 4RS) equivalent to a total area of 103,812 km^2.

MATERIAL AND METHODS

Model structure

Under the CDEENA program, mass-balance models using Ecopath (Christensen and Pauly 1993; Bundy et al. 2000) and inverse methodology (Vézina and Platt 1988; Savenkoff et al. 2001) have been constructed for different ecosystems in Atlantic Canada and for different time periods. These models, as opposed to traditional approaches, consider the ecosystem as a whole rather than its components separately and thus provide a description of trophic interactions between all functional groups of the ecosystem. The models generate a "snapshot" of the system at one time and use mass-balance principles to estimate flows of organic matter or energy among components of an ecosystem.

Ecopath is a widely used software that develops flow networks based on biomass and energetic data. Ecopath flow network solutions are not unique because often the ecosystem-level information is incomplete (underdetermined system). We therefore need to use different approaches with the same data to ascertain the robustness of estimated flow networks. The inverse approach solves flow networks by finding the solution that minimizes (objective least-squares criterion) both the sum of squared flows (thus the total sum of flows through the food web) and the sum of squared residual errors ε (minimizes the imbalances between inputs and outputs) consistent with the constraints (Vézina and Platt 1988; Savenkoff et al. 2001).

Under the steady-state assumption, consumption, representing the input, must balance the sum of the outputs consisting of production, respiration, and egestion (non-assimilated food, feces, or detrital flow) for each individual compartment. Consumption represented ingestion of prey both from within and outside the system (i.e., import).

$$\text{Consumption} = \text{production} + \text{egestion} + \text{respiration} \quad (1)$$

Production of a given group included biomass accumulation as well as the biomass lost to natural mortality (predation, disease, and other natural causes of death) and export. Export from a group consisted of catches (fishing mortality) and net migration (emigration and immigration, food intake by predators that are not part of the system, etc.).

$$\text{Production} = \text{biomass accumulation} + \text{predation} + \text{other mortality} + \text{export} \quad (2)$$

Assuming that there were no year-to-year changes in biomass over the 1994–1996 time period and that net migration was zero, production was simply the biomass lost to predation, natural mortality other than predation, and fishing mortality. Finally, the general mass-balance equation for individual compartments can be written as:

$$\text{Consumption} - \text{egestion} - \text{respiration} - \text{predation} - \text{other mortality} - \text{fishing mortality} = 0 + \varepsilon \quad (3)$$

The equations calculated for this study were not "absolutely" balanced, that is, the sum of the inputs and outputs for each compartment did not necessarily equal zero. We refer to these differences as residuals, which are represented by the error term ε. Inverse modelling can thus find a solution that was not necessarily balanced (not in steady state).

For phytoplankton and detritus, the general mass-balance equation was simplified. For the phytoplankton group, the net (corrected for respiration) production must balance the sum of the outputs (phytoplankton mortality including the egestion term and consumption of phytoplankton). For the detritus group, the inputs (egestion and other natural causes of death for other groups) must balance the sum of the outputs (consumption of detritus, bacterial remineralization of detritus, and burial). As bacteria were considered part of the detritus, detritus is assumed to respire.

With the compartmental mass-balance equations, the general structure of an inverse model also includes data equations and constraints. The data equations attempt to fix the value of certain flows or combination of flows (e.g., incorporate the observations into the model that coincide with the period/region for which a solution was tested) while the constraints incorporate general knowledge into the model. The input data introduced directly into the model as data equations included values for exports (catches) from the system, production, and diet proportions locally estimated from field studies. Data equations are also used for diet proportions available only as point estimates (no variance estimate) or with low observed values (i.e., <0.5%) and low uncertainty (i.e., SD < 0.6%). The system of equations above was strongly underdetermined, so additional constraints (other conditions that reflect our prior knowledge of this system) were added to obtain a meaningful solution. Each flow was taken to be non-negative, and the flows and ratios of flows (metabolic efficiencies) were assumed to fall within certain ranges to satisfy basic metabolic requirements. Gross growth efficiency (GE) is the ratio of production to consumption and for most groups should have values between 10 and 30% (Christensen and Pauly 1992). Exceptions are top predators, e.g., marine mammals and seabirds, which can have lower GE (between 0.1 and 1%), and small, fast growing fish larvae or nauplii or bacteria, which can have higher GE (between 25 and 50%) (Christensen and Pauly 1992). Following Winberg (1956), 80% of the consumption was assumed to be physiologically useful for carnivorous fish groups while the non-assimilated food (20%, consisting of urine and feces) was directed to the detritus. For herbivores, the proportion not assimilated could be considerably higher, e.g., up to 40% in zooplankton (Christensen and Pauly 1992). We constrained the assimilation efficiency (AE) to fall between 70 and 90% for all groups except for large and small zooplankton (between 50 and 90%).

Certain flows have a minimal and maximal value imposed (export for detritus, production, consumption, diet composition, etc.). The production and consumption values that were not estimated from local field studies were incorporated as constraints. The other diet proportions with higher values (i.e., >0.5%) were also specified as constraints. To facilitate comparisons with Ecopath models, we added constraints on the ecotrophic efficiency (EE). The ecotrophic efficiency is the fraction of the production that is either passed up the food web or exported. These values should be between 0 and 0.95 (Christensen and Pauly 1992, 1998). Here, a value only slightly above zero indicates that the group is not consumed in noticeable amounts by any other group in the system (e.g., top predators). Conversely, a value near or equal to 0.95 indicates that the group is heavily preyed upon and/or highly exploited by a fishery, leaving no individuals to die of other causes (small prey organisms).

We perturbed the data within their uncertainty range and the unconstrained part of the solution could move within the a priori bounds. By randomly perturbing data inputs, we constructed a set of balanced solutions and we used the mean of these 31 random perturbations (including a response without perturbation).

Study area

The study covers an area of the northern Gulf of St. Lawrence (NAFO divisions 4RS), equivalent to 103,812 km^2 (Fig. 1). The nearshore region (depths < 37 m) was not included in the model. Infra-littoral species and American lobster (*Homarus americanus*) were not included in this study. This zone was excluded from the model because exchanges between infra-littoral and pelagic zones are still poorly understood. The official sampling area used in our models for the calculation of densities represented the surface of strata sampled during the summer scientific survey in the northern Gulf of St. Lawrence. The period covered by this analysis was from 1994 to 1996, after the groundfish collapsed.

Functional groups

Based on data availability and the ecological and commercial significance of the species, the trophic food web is depicted by a number of compartments or functional groups representing the main pelagic, demersal, and benthic species present, which are interconnected by mass flows of matter. The whole-system model of the northern Gulf of St. Lawrence was divided into 32 functional groups or compartments (Table 1). We distinguished five marine mammal groups, one seabird group, sixteen fish groups, eight invertebrate groups, one phytoplankton group, and one detritus group (Table 1). Some groups such as large pelagic feeders and large demersal feeders are composite groups, where the species were aggregated on the basis of similarity in size and ecological role. Cod and Greenland halibut were each separated into two groups based on diet, age/size at first capture, and age/size at maturity. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but for this model it was assumed that the change occurs at 35 cm for cod (Lilly 1991) and 40 cm for Greenland halibut (Bowering and Lilly 1992). Due to a lack of data, we could not distinguish juveniles and adults for other fish species.

Collecting the data

All parameter estimations were made within a collaborative framework, in which experts for the various functional groups were consulted. A considerable effort was expended to obtain input data in the study area and during the period of interest. However, information on several groups (e.g., forage species, benthic invertebrates, and zooplankton) was sparse or non-existent for the area and period studied and was thus taken for the same area but for other time periods or from the literature for other areas and/or time periods. Based on these different sources of data (local and literature), we estimated the lower and upper limits of each input data used in inverse modelling. This process partly explains the high coefficients of variation for the production, consumption, and diet data (74, 89, and 133%, respectively) as well as those for biomass or export (66 and 75%, respectively).

Biomass

The biomass density (called biomass in this document) of a species (or group of species) was assumed to be constant for the 1994–1996 period modelled. The biomass of each box of the model was obtained directly or was estimated from similar ecosystems when it was not available for 4RS. This parameter is expressed in biomass per surface unit (i.e., tons wet weight km^{-2}). Biomass was estimated from sequential population analysis or scientific trawl survey data for most groups.

An annual summer trawl survey for groundfish has been conducted since 1990 in the northern Gulf aboard the CCGS *Alfred Needler*. The sampling strategy used consisted in a stratified random sampling following predetermined strata based on depth (Doubleday 1981). Stratified random means were calculated to estimate the biomass in the area using the *PACES* (*Programme d'Analyse des Campagnes d'Échantillonnage Stratifiées*) software (Bourdages 2001).

In 1990, the vessel and gear used for the survey changed. From 1984 to 1990, the survey was conducted on the *Lady Hammond* with a Western IIA trawl. Since 1990, the survey was done using a URI 81/114 trawl aboard the CCGS *Alfred Needler*. A comparative study was conducted during the 1990 survey in order to assess the relative efficiency of both vessels and gears. The relative efficiency between gears and vessels was estimated by a general linear model assuming a Poisson distribution of error with an extra parameter for an extra Poisson distribution as developed by Swain (Gulf Fisheries Centre, DFO, Moncton, unpublished data). The length–frequency data collected during the 1994–1996 period were corrected for catchability so that they were similar to those sampled during the 1985–1987 period. However, information was not available for different species or functional groups. Thus, different models were assumed to describe them (Table 2). Also, the use of trawl data to estimate biomass of fish species suffers from inherent problems due to variable catchability of the different species considered. Different species have different degrees of catchability by the fishing gear, making comparison of biomass estimates among species difficult. Trawlable biomass estimates were converted to catchability-adjusted biomass based on catchability coefficients estimated by Harley and Myers (2001). Length-specific corrections were applied to numbers-at-length data before they were converted to biomass estimates. In this way, we hope to lessen the impact of catchability on the biomass estimates and render data comparable between species (Table 3).

To estimate the biomass of younger age classes not captured in the survey, numbers-at-age were back-calculated from a known number of the first year class captured in the survey, assuming a natural mortality rate, and then multiplying by mean mass-at-age to obtain mean biomass-at-age.

Standard deviations for biomass and catch were based only on the variations in the point estimates for the three years in each period (i.e., error in the estimates themselves was not included in these SDs)

Table 1. Functional groups used in modelling for the 1994–1996 period in the northern Gulf of St. Lawrence.

Group Name	Main species
Cetaceans	*Balaenoptera physalus*, *Balaenoptera acutorostrata*, *Lagenorhynchus acutus*, *Lagenorhynchus albirostris*, *Megaptera novaeangliae*, *Phocoena phocoena*
Harp seals	*Phoca groenlandica*
Hooded seals	*Cystophora cristata*
Grey seals	*Halichoerus grypus*
Harbour seals	*Phoca vitulina*
Seabirds	*Alca torda*, *Cepphus grylle*, *Fratercula arctica*, *Larus argentatus*, *L. delwarensis*, *L. marinus*, *Morus bassanus*, *Oceanodroma leucorhoa*, *Phalacrocorax auritus*, *P. carbo*, *Sterna hirundo*, *S. paradisaea*, *Rissa tridactyla*, *Uria aalge*
Large Atlantic cod (> 35 cm)	*Gadus morhua*
Small Atlantic cod (≤ 35 cm)	*Gadus morhua*
Large Greenland halibut (> 40 cm)	*Reinhardtius hippoglossoides*
Small Greenland halibut (≤ 40 cm)	*Reinhardtius hippoglossoides*
American plaice	*Hippoglossoides platessoides*
Flounders	*Glyptocephalus cynoglossus*, *Limanda ferruginea*, *Paralichthys oblongus*, *Pseudopleuronectes americanus*
Skates	*Amblyraja radiata*, *Malacoraja senta*, *Leucoraja ocellata*
Redfish	*Sebastes fasciatus*, *S. mentella*
Large demersal feeders	*Anarhichas* spp., *Centroscyllium fabricii*, *Cyclopterus lumpus*, *Hippoglossus hippoglossus*, *Lophius americanus*, *Melanogrammus aeglefinnus*, *Urophycis tenuis*, *Lycodes* spp., Macrouridae, Zoarcidae
Small demersal feeders	*Argentina* spp., *Emicrotremus* spp., *Macrozoarces americanus*, *Myoxocephalus* spp., *Tautogolabrus adspersus*, Bleniidae, Cottidae, Phjolidae, Zoarcidae, juvenile large demersal feeders
Capelin	*Mallotus villosus*
Sand lance	*Ammodytes americanus*, *A. dubius*
Arctic cod	*Boreogadus saida*

Table 1. Cont.

Group Name	Main species
Large pelagic feeders	*Cetorhinus maximus*, *Merluccius bilinearis*, *Pollachius virens*, *Squalus acanthias*, *Thunnus thynnus*
Piscivorous small pelagic feeders	*Illex illecebrosus*, *Scomber scombrus*, piscivorous myctophids and other mesopelagics, piscivorous juvenile large pelagic feeders
Planktivorous small pelagic feeders	*Clupea harengus harengus*, *Gonatus* spp., *Scomberesox saurus*, planktivorous myctophids and other mesopelagics, planktivorous juvenile large pelagic feeders
Shrimp	*Pandalus borealis*, *P. montagui*
Large crustaceans	*Chionoecetes opilio*, other non-commercial species (*Hyas* spp.)
Echinoderms	*Echinarachnius parma*, *Ophiura robusta*, *Stronglyocentrotus pallidus*
Molluscs	*Cyrtodaria siliqua*, *Mesodesma deauratum*
Polychaetes	*Exogene hebes*
Other benthic invertebrates	Miscellaneous crustaceans, nematodes, other meiofauna
Large zooplankton (> 5 mm)	Euphausiids, chaetognaths, hyperiid amphipods, cnidarians and ctenophores (jellyfish), mysids, tunicates >5 mm, ichthyoplankton
Small zooplankton (< 5 mm)	Copepods (mainly *Calanus finmarchicus*, *C. hyperboreus*, and *Oithona similis*), tunicates < 5 mm, meroplankton
Phytoplankton	Diatom species such as *Chaetoceros affinis*, *Chaetoceros* spp., *Fragilariopsis oceanica*, *F. cylindrus*, *Leptocylindrus minimus*, *Thalassiiosira bioculata*, T. *nordenskioldii*, *T. pacifica*, *T. punctigera*, and a mixture of autotrophic and mixotrophic organisms including Cryptophytes, dinoflagellates, Prasinophytes, Prymnesiophytes, and mixotrophic *Stombidium* spp.
Detritus	Sinking particulate organic matter including both large particles (consisting of animal carcasses and debris of terrigenous and coastal plants) and fine particles (mostly from planktonic organisms, including feces, moults, phytoplankton aggregates, bacteria)

Production

Production is the total amount of tissue produced in the population or community under study during a given time period (Christensen and Pauly 1992). It includes all living matter produced by a group (even if it is finally consumed, fished, or lost to other mortality) during the model period. In the northern Gulf of St. Lawrence model, it was assumed that there was no year-to-year change in biomass over the 1994–96 time period and that emigration was zero. Thus production in this model is simply the biomass that is lost to natural mortality (predation, disease, and other natural causes of death) and fishing mortality. P/B is the ratio of production (P) to biomass unit (B). Absolute production is a flux expressed in biomass per surface unit per year (e.g., t km^{-2} yr^{-1}).

The means and SDs for production values were based on (1) the two extreme values (when different approaches were used to calculate them and using biomass values from the three years) or (2) all the point estimates (when a single approach was used and using biomass values from the three years).

Consumption

Consumption is defined as the utilization of food by a group during the time period considered by the model (Christensen and Pauly 1993). Q/B is the ratio of consumption (Q) to biomass (B). Absolute consumption is a flux expressed in biomass per surface area per year (e.g., t km^{-2} yr^{-1}).

Consumption was estimated from field studies where possible, either from the region or for species from similar areas reported in the literature. In addition, models were used to estimate consumption by marine mammals (Hammill and Stenson, 2000) and seabirds (G. Chapdelaine, Environment Canada, Migratory Birds Division, Sainte-Foy, Québec, unpublished data).

Where this was not possible, consumption values were taken either from the literature and/or estimated assuming a gross growth efficiency (GE; the ratio of production to consumption) ranging between 10 and 30% (Christensen and Pauly, 1992).

The means and SDs were calculated on the two extreme values.

Table 2. Relative efficiency (R) for each fish species or functional group between both gears and vessels during the 1985–1987 (*Lady Hammond* vessel using a Western IIA trawl) and the 1994–1996 (CCGS *Alfred Needler* using URI 81/114 trawl) periods. L: length in cm.

Species	Relative efficiency	Associated groups
Cod	$R = \exp(-3.8095+5.3371*\exp(-0.00995*L))$	
Haddock	$R = \exp(2.80893–0.06843*L)$	Black dogfish, and large pelagic feeders
White hake	$R = \exp(1.75615–0.03891*L)$	Longfin hake, marlin spike, wolffish, eelpout, monkfish, lumpfish, grenadier, Arctic cod, and small demersal feeders
Redfish	$R = \exp(-0.5386+6.0832*\exp(-0.1138*L))$	
American plaice	$R = \exp(-0.95062+0.000867*L)$	
Witch flounder	$R = \exp(-0.75+23.5989*\exp(-0.2196*L))$	Flounders and skates
Greenland halibut	$R = \exp(1.58086-0.04333*L)$	

Table 3. Catchability factors (Q) used to estimate biomass of fish species from trawl data. L: length in cm.

Species or species group	Catchability coefficient	Associated species
Cod	$Q = \frac{0.949 * \exp(-5.06 + 0.139 * L)}{1 + \exp(-5.06 + 0.139 * L)}$	
Haddock	$Q = \frac{1.59 * \exp(-2.77 + 0.0646 * L)}{1 + \exp(-2.77 + 0.0646 * L)}$	
Demersal gadoids	$Q = \frac{1.04 * \exp(-3.47 + 0.0914 * L)}{1 + \exp(-3.47 + 0.0914 * L)}$	Grenadiers, fourbeard rockling, eelpouts, longfin hake, white hake, large headed (L x 1.25; sculpins, lumpfish, wolffish, sea raven), small headed (L x 0.75; seasnails, spiny lumpsucker)
Pelagic gadoids	$Q = \frac{0.64 * \exp(-4.58 + 0.0785 * L)}{1 + \exp(-4.58 + 0.0785 * L)}$	Spiny dogfish, silver hake, pollock, redfish (L x 1.25)
Flatfish	$Q = \frac{0.986 * \exp(-4.43 + 0.109 * L)}{1 + \exp(-4.43 + 0.109 * L)}$	Greenland halibut, American plaice, flounders, skates (L x 1.25)

Diet composition

Diet matrices were constructed using field data from the study area whenever possible. However, these data do not exist for some species. For these species, diet data were taken for the same area but for another time period or from the literature for other areas and/or time periods. Using all the available field samples or literature reports, the minimum and maximum values observed for each diet proportion were used as inputs for inverse modelling. Means and standard deviations were calculated either directly from the lower and upper limits when there was no information on number of stomachs (mean and SD of the two extreme values) or from the different diet proportions, which were weighted by the number of stomachs when stomach content analyses were given (mean and SD of all the point estimates). The diet outputs estimated by the balanced (optimized) solution of inverse modelling were then used as inputs for the Ecopath model. In the diet tables, empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts (<0.1%) or that this represented a potential trophic relation between prey and predator in other ecosystems or another period of time (equal to 0%). There was a large number (62 of 356 flows) of such values during the mid-1990s.

FishBase

Occasionally, information was not available for some parameters. When this happened we referred to FishBase (Froese and Pauly 2002), which is a biological database developed at the International Centre for Living Aquatic Resources Management (ICLARM) in collaboration with FAO and other organizations. It includes information on fish species and is updated frequently with regards to information such as maximum size, growth parameters, natural mortality, and standardized diet composition (Froese and Pauly 1995).

RESULTS: DATA GATHERING AND SYNTHESIS

In this section, each functional group of the northern Gulf of St. Lawrence ecosystem is described along with respective estimates of biomass, production, consumption, and diet composition that are used as inputs for modelling.

Cetacea

Background

The northern Gulf of St. Lawrence is dominated by boreal cetaceans ranging from large and medium-sized mysticetes and odontocetes to small odontocetes such as porpoises and dolphins (Kingsley and Reeves 1998). Minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), long-finned pilot (*Globicephala melas*), and humpback (*Megaptera novaeangliae*) whales are the most abundant species among the large and medium whales. The harbour porpoise (*Phocoena phocoena*) is the most abundant of the small dolphins in the Gulf while white-sided dolphins (*Lagenorhynchus acutus*) and white-beaked dolphins (*Lagenorhynchus albirostris*) also occur in this area (Kingsley and Reeves 1998). The cetacean survey of the Gulf of St. Lawrence (Kingsley and Reeves 1998) covered 221,950 km^2, so we used this inventory area to calculate the parameters for this group instead of the value habitually used for the other groups (the sampling area for divisions 4RS).

Catch

Canada ceased commercial whaling in 1972 and there has been no hunt since for subsistence purposes in 4RS. However, information from a questionnaire survey conducted in 1989 and 1990 in the Gulf (4RST) indicated an annual average incidental catch from fishing gear of 1,835 harbour porpoises (Fontaine et al. 1994a). This is equivalent to a catch of 92 tons within a 221,950 km^2 sampling area ($3.75 \times 10^{-4} \pm 2.09 \times 10^{-5}$ t km^{-2} yr^{-1}). The final solution of inverse modelling (hereafter termed "inverse solution") estimated a catch of 3.70×10^{-4} t km^{-2} yr^{-1}.

Biomass

Aerial survey estimates of cetacean abundance in the Gulf of St. Lawrence, not corrected for visibility bias, are available for the summer of 1995 (Kingsley and Reeves 1998). The area of the strata corresponding to the northern Gulf covers 144,468 km^2. The density in this zone is applied to the present study zone. These estimates were adjusted by a factor of 1.09 to account for animals that were potentially visible to the observers but were not seen (Marsh and Sinclair 1989) and by a factor of 2.27 to account for animals missed owing to water turbidity (Marsh and Sinclair 1989). These adjustments resulted in abundance estimates of 297 humpback whales, 990 fin whales, 2,128 minke whales, 3,019 long-finned pilot whales, 21,427 harbour porpoises, 17,419 white-sided dolphins, and 6,532 white-beaked dolphins. Other whales, like blue whales for instance, were present in the survey of the Gulf of St. Lawrence but were seen too infrequently to allow any estimation of their biomass.

Mean body mass taken from the literature was 31 t for humpback whales (averaged from Hay [1985], Martin [1990], and Kenney et al. [1997]); 38.5 t for fin whales, 5.6 t for minke whales, 1.4 t for long-finned pilot whales, and 0.05 t for harbour porpoises (averaged from Lien [1985], Martin [1990], and Kenney et al. [1997]); 0.13 t for white-sided dolphins (Sergeant et al. 1980); and 0.217 t for white-beaked dolphins (Ridgway and Harrison 1999). To calculate biomass, we used a population growth rate of 6.5% for humpback whales (Barlow and Clapham 1997), 6.7% for fin whales (Bundy et al. 2000), 6.7% for minke whales (Bundy et al. 2000), 4.0% for long-finned pilot whales (Waring et al. 1999), 9.0% for harbour porpoises (Caswell et al. 1998), 2.0% for white-sided dolphins (Heise 1997), and 2.0% for white-beaked dolphins (Heise 1997). For harbour porpoises, an annual incidental catch of 581 individuals was also used. Assuming a residence time of 180 days for all whales within the potential area of Kinglsley and Reeves (1998) (144,468 km^2), the average annual biomass was 33,677 tons or 0.233 ± 0.014 t km^{-2}.

Production

Production was assumed to be equivalent to the biomass multiplied by natural mortality (M), plus catch. Natural mortality for a combination of cetaceans was estimated to range between 0.074 (Tanaka 1990) and 0.075 (Ohsumi 1979), and the mean annual catch used was 3.75×10^{-4} t km^{-2} yr^{-1} (Fontaine et al. 1994a). This resulted in a total annual production of 0.018 t km^{-2} yr^{-1} (range: 0.017–0.019 t km^{-2} yr^{-1}). Based on the annual consumption reported by Trites et al. (1997) (see below) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic), we obtained another production value of 0.013 t km^{-2} yr^{-1}. Based on these different estimates, the mean production value was 0.016 ± 0.004 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.015 t km^{-2} yr^{-1}, representing a P/B of 0.06 yr^{-1}.

Consumption

The daily consumption by cetaceans was calculated using:

$$R = 0.1W^{0.8} \quad (4)$$

where R is the daily ration for an individual in kg and W is the mean body mass in kg (Trites et al. 1997). Assuming a residence time of 180 days, the annual consumption by species was 0.145 t km^{-2} yr^{-1} for humpback whales, 0.575 t km^{-2} yr^{-1} for fin whales, 0.264 t km^{-2} yr^{-1} for minke whales, 0.124 t km^{-2} yr^{-1} for long-finned pilot whales, 0.061 t km^{-2} yr^{-1} for harbour porpoises, 0.107 t km^{-2} yr^{-1} for white-sided dolphins, and 0.060 t km^{-2} yr^{-1} for white-beaked dolphins. This gives a mean annual consumption of 1.337 ± 0.074 t km^{-2} yr^{-1} (range: 1.264–1.412 t km^{-2} yr^{-1}). Gross growth efficiency (GE = P/Q) ranges between 0.1 and 1% for marine mammals (Christensen and Pauly 1992). Based on the previous total annual production (0.016 t km^{-2} yr^{-1}) and the GE limits, we obtained two other consumption values of 1.606 and 16.064 t km^{-2} yr^{-1}. The value based on the lower GE limit was not realistic, so the resulting consumption range was 1.264 and 1.606 t km^{-2} yr^{-1}. The mean consumption value was 1.435 ± 0.242 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.514 t km^{-2} yr^{-1}, representing a Q/B of 6.493 yr^{-1}.

Diet composition

Unfortunately, there are few quantitative descriptions of diet for cetaceans. Where the literature refers to prey using terms such as "preponderant" or "predominant," it was assumed that they make up at least 75% of consumption by mass. If other prey were reported, remaining consumption was divided equally among them. Based on the literature, the following diets were used in the analysis:

- Humpback whales: capelin, sand lance, squid, and euphausiids (Mitchell 1973);
- Fin whales: capelin, sand lance, herring, and euphausiids (Mitchell 1975);
- Minke whales: capelin, small cod, herring, squid, and euphausiids (Horwood 1990);
- Long-finned pilot whales: squid, juvenile cod, and capelin (Lien 1985);
- Harbour porpoises: capelin, herring, redfish, mackerel, cod, squid, and sand lance (Fontaine et al., 1994b);
- White-sided dolphins: herring, squid, smelt, silver hake, and crustaceans (Katona et al. 1978);
- White-beaked dolphins: cod, whiting, mackerel, and cephalopods (Santos et al. 1994).

In order to calculate the overall proportion of each prey item by mass, total consumption by prey type was first calculated and overall proportions weighted according to the consumption of each cetacean species. Due to the uncertainties with diet data, we also used a diet composition from the Newfoundland–Labrador Shelf (1985–1987 period) (Bundy et al. 2000) (Table 4).

Table 4. Diet composition of cetaceans used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Cetaceans				
Prey	Mean	±SD	Min	Max	Est
Large cod	**0.2**	0.2	0.0	0.3	0.2
Small cod	1.1	1.4	**0.0**	**1.9**	0.0
Large Green. halibut					
Small Green. halibut					
American plaice	**0.0**	0.0	0.0	0.0	0.0
Flounders					
Skates					
Redfish	**0.1**	0.2	0.0	0.3	0.1
Large demersals	2.2	1.9	**0.6**	**3.3**	1.0
Small demersals	1.8	2.3	**0.0**	**3.3**	0.3
Capelin	58.1	5.8	**48.9**	**57.1**	56.8
Sand lance	**5.3**	0.5	4.5	5.2	5.3
Arctic cod					
Large pelagics	**0.2**	0.3	0.0	0.4	0.2
Pisci. small pelagics	9.7	12.5	**0.0**	**17.6**	6.7
Plank. small pelagics	7.9	6.0	**3.0**	**11.5**	10.5
Shrimp	**0.1**	0.1	0.0	0.1	0.1
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	8.8	3.4	**5.6**	**10.4**	10.4
Small zooplankton	4.6	5.9	**0.0**	**8.3**	8.3
Phytoplankton					
Detritus					
Total	100.0		62.7	119.7	100.0
TRN	14				

Seals

Background

Four species of pinnipeds are common in the Gulf of St. Lawrence. The harp seal (*Phoca groenlandica*) is the most abundant pinniped in Atlantic Canada and usually summers in the Canadian Arctic or northwest Greenland before returning south to overwinter in Canadian Atlantic waters. Reproduction occurs in March on the pack ice in the Gulf of St. Lawrence (Gulf herd) and off southern Labrador (Front herd). In the Gulf, animals whelp in two areas: off the lower North Shore and near the Îles-de-la-Madeleine (Sergeant 1991). During the 1994–1996 period, the northwest Atlantic population was estimated to be 5,037,255 (Healey and Stenson 2000), with an average of 2.5% of the pups, 2.5% of juveniles, and 4.1% of the adults found in the northern Gulf of St Lawrence (Hammill and Stenson 2000).

Hooded seals (*Cystophora cristata*), which are larger than harp seals, are the least abundant pinniped within the study area, with an average population of 13,459 individuals for 1994–1996 (Hammill, DFO, Institut Maurice-Lamontagne, Mont-Joli, Québec, unpublished data). Only 36.2% of the animals are situated in divisions 4RS (Hammill and Stenson 2000). In the northwest Atlantic, most pups are born in March on pack ice off northeast Newfoundland, with smaller whelping concentrations located in Davis Strait and the Gulf of St. Lawrence. After leaving the whelping patch in late March, adults from the Gulf of St. Lawrence move to the northern Gulf where they remain until mid-May, when they return to Greenland. Hooded seals have been protected in the Gulf since 1972 (Hammill et al. 1997).

The grey seal (*Halichoerus grypus*) is slightly smaller than the hooded seal. Major breeding colonies in eastern Canada are located on Sable Island and in the southern Gulf of St. Lawrence (Mansfield and Beck 1977). After breeding, both juveniles and adults disperse widely over eastern Canada. Large numbers are known to feed in the northern Gulf of St. Lawrence, which makes it the second most abundant pinniped of the zone (Hammill and Stenson 2000). The population in 1994–1996 averaged 67,690 individuals from the Gulf herd and 100,263 individuals from the Sable Island herd (M. Hammill, unpublished data), with 33.7% of the Gulf herd and 7.9% of the Sable Island herd found in divisions 4RS (Hammill and Stenson 2000).

Harbour seals (*Phoca vitulina*) are found throughout eastern Canada (Boulva and McLaren 1979), occurring in small groups dispersed along coastal areas (Lesage et al. 1995). Harbour seal abundance in Atlantic Canada has never been evaluated by direct survey. Based on questionnaires sent to fisheries officers, Boulva and McLaren (1979) estimated about 13,000 animals in eastern Canada. Hammill and Stenson (2000) modelled population changes for this species and estimated that the average population was 30,163 for 1994–1996 (M. Hammill, unpublished data), with 26.4% of animals situated in the northern Gulf (Hammill and Stenson 2000).

Catch

Commercial catches (total numbers) for harp, grey, and hooded seals are reported in the Atlantic resource management landing reports (Stenson et al. 2000). Catches were divided into pups (young of the year) and animals one year and older (Sjare et al. 1996). Numbers-at-age were multiplied by mean mass-at-age (Hammill and Stenson 2000) to obtain total catches in tons. For

harp seals, the mean annual catch for 1994–1996 was estimated at $1.54 \times 10^{-2} \pm 1.44 \times 10^{-2}$ t km^{-2} yr^{-1}. The inverse solution estimated a catch of 7.94×10^{-3} t km^{-2} yr^{-1}.

The number of hooded seals removed from the northern Gulf of St. Lawrence (data from the west coast of Newfoundland, the Gulf, and Québec's North Shore) was obtained directly from catch statistics. The mean annual catch was estimated to be $2.02 \times 10^{-5} \pm 1.98 \times 10^{-5}$ t km^{-2} yr^{-1}. The inverse solution estimated a catch of 2.27×10^{-5} t km^{-2} yr^{-1}.

The grey seal is not hunted commercially in Canadian waters. However, this species is subject to a scientific removal and bounty hunting. Harvesting activity has declined over the last 50 years and the bounty was eliminated in 1992 (Hammill et al. 1998). These removals resulted in an estimated mean annual catch of $1.22 \times 10^{-5} \pm 2.12 \times 10^{-5}$ t km^{-2} yr^{-1}. The inverse solution estimated a catch of 1.29×10^{-5} t km^{-2} yr^{-1}.

Even though harbour seals have been protected since 1976 (Boulva and McLaren 1979), some losses may have occurred through by-catch by commercial fisheries. However, there is no data available to assess this loss, so catch was assumed to be negligible.

Biomass

Biomass was estimated by multiplying abundance by mean mass-at-age (Hammill and Stenson 2000). The number of seals in each age class was obtained from an updated version of the population model of Hammill and Stenson (2000). Biomass was adjusted for residence time in 4RS (Hammill and Stenson 2000), resulting in mean annual biomass estimates for the 1994–1996 period of 0.127 ± 0.005 t km^{-2} for harp seals, 0.005 ± 0.000 t km^{-2} for hooded seals, 0.035 ± 0.002 t km^{-2} for grey seals, and 0.004 ± 0.000 t km^{-2} for harbour seals. Note that the standard deviation for each seal group was only the variation in the point estimates for the three years of the 1994–1996 period.

Production

The P/B ratio was estimated by dividing the pup biomass by the uncorrected population biomass (minimum value) for the northern Gulf of St. Lawrence as reported in an updated version of the population model of Hammill and Stenson (2000) for the 1994–1996 period. The P/B ratios were 0.066 yr^{-1} for harp seals, 0.061 yr^{-1} for hooded seals, 0.078 yr^{-1} for grey seals, and 0.071 yr^{-1} for harbour seals. This resulted in production values of 0.014 ± 0.000 t km^{-2} yr^{-1} for harp seals, 0.0003 ± 0.0000 t km^{-2} yr^{-1} for hooded seals, 0.0027 ± 0.0001 t km^{-2} yr^{-1} for grey seals, and 0.0003 ± 0.0000 t km^{-2} yr^{-1} for harbour seals. Based on the annual consumption values of Hammill and Stenson (2000) (see below) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic), we obtained other production values: 0.006 t km^{-2} yr^{-1} for harp seals, 0.0006 t km^{-2} yr^{-1} for hooded seals, 0.0011 t km^{-2} yr^{-1} for grey seals, and 0.0002 t km^{-2} yr^{-1} for harbour seals. Based on each upper and lower limit range, we obtained mean annual production values of 0.010 ± 0.006 t km^{-2} yr^{-1} for harp seals, 0.0005 ± 0.0002 t km^{-2} yr^{-1} for hooded seals, 0.0020 ± 0.0012 t km^{-2} yr^{-1} for grey seals, and 0.0002 ± 0.0001 t km^{-2} yr^{-1} for harbour seals. The inverse solution estimated production values of 0.009 t km^{-2} yr^{-1} (P/B = 0.074

yr^{-1}) for harp seals, 0.0005 t km^{-2} yr^{-1} (P/B = 0.090 yr^{-1}) for hooded seals, 0.0018 t km^{-2} yr^{-1} (P/B = 0.052 yr^{-1}) for grey seals, and 0.0002 t km^{-2} yr^{-1} (P/B = 0.053 yr^{-1}) for harbour seals.

Consumption

Total annual consumption of prey by each seal species in the study area was estimated from an updated version of the consumption model of Hammill and Stenson (2000). The mean annual consumption values were 0.553 ± 0.020 t km^{-2} yr^{-1} for harp seals, 0.065 ± 0.003 t km^{-2} yr^{-1} for hooded seals, 0.111 ± 0.012 t km^{-2} yr^{-1} for grey seals, and 0.017 ± 0.001 t km^{-2} yr^{-1} for harbour seals. The annual consumption ranges were 0.532–0.573 t km^{-2} yr^{-1} for harp seals, 0.062–0.068 t km^{-2} yr^{-1} for hooded seals, 0.068–0.153 t km^{-2} yr^{-1} for grey seals, and 0.016–0.018 t km^{-2} yr^{-1} for harbour seals. Based on the mean annual production estimated from Hammill and Stenson (2000) (see above) and the upper GE limit (1%; values based on the lower GE limit of 0.1% were not realistic), we obtained other consumption values: 0.974 t km^{-2} yr^{-1} for harp seals, 0.048 t km^{-2} yr^{-1} for hooded seals, 0.196 t km^{-2} yr^{-1} for grey seals, and 0.024 t km^{-2} yr^{-1} for harbour seals. Finally, based on these different values, we estimated the lower and upper consumption limits used as constraints in inverse modelling. The resulting mean consumption values of each upper and lower limit range were 0.753 ± 0.312 t km^{-2} yr^{-1} for harp seals, 0.058 ± 0.014 t km^{-2} yr^{-1} for hooded seals, 0.132 ± 0.091 t km^{-2} yr^{-1} for grey seals, and 0.020 ± 0.006 t km^{-2} yr^{-1} for harbour seals. The inverse solution estimated consumption values of 1.046 t km^{-2} yr^{-1} (Q/B = 8.207 yr^{-1}) for harp seals, 0.056 t km^{-2} yr^{-1} (Q/B = 10.775 yr^{-1}) for hooded seals, 0.183 t km^{-2} yr^{-1} (Q/B = 5.296 yr^{-1}) for grey seals, and 0.024 t km^{-2} yr^{-1} (Q/B = 5.699 yr^{-1}) for harbour seals.

Diet composition

For harp seals, diet information was available for nearshore waters of the northwest Atlantic during 1990–1993 (Lawson et al. 1995), for inshore 2J3KL during 1991–1992 (Lawson et al. 1993), and for the St. Lawrence Estuary (Murie and Lavigne 1991; Beck et al. 1993; Lawson et al. 1995; Hammill and Stenson 2000). According to these diet studies, the main prey species were, in order of importance, capelin, Atlantic herring, Atlantic cod, redfish, and Arctic cod.

There was no local diet information available for hooded seals in the northern Gulf. Hammill et al. (1997) used a diet based on work done by Ross (1993), where the main prey items were young Greenland halibut, flounders, and small pelagic feeders. Other information about this species was based on offshore samples from NAFO divisions 2J3KL collected from 1991–1993 (Lawson et al. 1993). In that study, stomachs examined contained mainly Atlantic cod, witch flounder, and squid. Hammill and Stenson (2000) used a diet made up of samples from Ross (1993) and Lawson and Stenson (DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data) in which major prey for the Gulf and 2J3KL inshore regions were Greenland halibut, redfish, Arctic cod, and herring.

Several studies have examined the diet composition of grey seals in the northern Gulf of St. Lawrence. These have determined that Atlantic cod, herring, lumpfish, wolffish, capelin, mackerel, and ocean pout were the main prey items of this species (Benoit and Bowen 1990; Murie and Lavigne 1992; Proust 1996; Hammill and Stenson 2000).

Harbour seal diet composition was examined in two inshore habitats of Atlantic Canada (lower Bay of Fundy and the north eastern coast of Nova Scotia) between 1988 and 1992 (Bowen and Harrison 1996). For the 250 food-containing stomachs examined, the major prey were Atlantic herring, squid, pollock (*Pollachius virens*), and Atlantic cod. The upper and lower limits resulting from these different diet studies are shown in Table 5.

Table 5. Diet compositions of seals used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. For groups with the CV indicated (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Harp seals					Hooded seals				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	1.2	2.8	**0.1**	**3.9**	1.5	10.5	14.7	**0.5**	**21.4**	14.5
Small cod	3.3	7.5	**0.0**	**10.7**	1.0	10.2	14.3	**0.5**	**20.8**	9.8
Large Green. halibut	2.0	4.7	**0.0**	**6.6**	1.9	1.7	2.5	**0.0**	**3.6**	1.7
Small Green. halibut	2.3	5.2	**0.0**	**7.4**	5.4	24.0	33.7	**1.3**	**48.9**	27.1
American plaice	4.1	9.4	**0.0**	**13.2**	9.2					
Flounders	6.8	15.7	**0.0**	**22.2**	0.0	14.6	21.6	**0.0**	**30.6**	7.3
Skates	**0.0**	0.0	0.0	0.0	0.0					
Redfish	4.6	10.5	**0.0**	**14.9**	8.2	13.1	12.4	**4.9**	**22.5**	13.6
Large demersals	3.3	7.6	**0.0**	**10.8**	0.0	1.2	1.7	**0.0**	**2.4**	1.2
Small demersals	2.2	4.0	**0.8**	**6.4**	0.8	5.7	8.5	**0.0**	**12.0**	5.7
Capelin	28.9	60.1	**4.6**	**89.6**	43.0	**0.5**	0.4	0.3	0.8	0.5
Sand lance	2.9	6.7	**0.0**	**9.5**	0.0					
Arctic cod	16.8	38.7	**0.0**	**54.7**	0.1	8.0	9.8	**1.4**	**15.3**	6.5
Large pelagics	**0.2**	0.3	0.0	0.5	0.2					
Pisci. small pelagics	2.2	5.0	**0.0**	**7.0**	0.0	3.4	5.1	**0.0**	**7.2**	4.8
Plank. small pelagics	6.1	14.1	**0.0**	**20.0**	0.4	7.0	10.4	**0.0**	**14.7**	7.2
Shrimp	2.1	4.8	**0.0**	**6.8**	2.2					
Large crustacea	1.7	3.9	**0.0**	**5.6**	1.2					
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	1.8	4.2	**0.0**	**5.9**	4.3					
Large zooplankton	7.6	17.4	**0.0**	**24.7**	20.6					
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		5.5	320.4	100.0	100.0		8.9	200.2	100.0
TRN	20					12				

Table 5. Cont.

	Grey seals					Harbour seals (CV= 50%)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod	10.5	15.4	**2.0**	**23.7**	13.4	3.4	2.3	**1.9**	**5.0**	4.4
Small cod	10.2	15.0	**1.9**	**23.1**	8.7	4.0	2.3	**2.4**	**5.6**	4.6
Large Green. halibut	**0.0**	0.0	0.0	0.0	0.0					
Small Green. halibut	**0.3**	0.5	0.0	0.7	0.3					
American plaice	5.1	8.7	**0.0**	**12.4**	11.7					
Flounders	8.0	13.8	**0.0**	**19.6**	3.0	1.8		**0.9**	**2.7**	2.3
Skates	16.6	28.7	**0.0**	**40.5**	13.3	**0.1**		0.1	0.2	0.1
Redfish	**0.0**	0.1	0.0	0.1	0.0	**0.4**		0.2	0.6	0.4
Large demersals	10.5	4.7	**9.5**	**16.2**	10.9	2.7		**1.3**	**4.0**	3.1
Small demersals	12.1	19.4	**1.1**	**28.5**	5.2	3.0		**1.5**	**4.4**	3.4
Capelin	8.3	13.6	**0.6**	**19.8**	12.3	5.9		**2.9**	**8.8**	7.0
Sand lance	5.5	9.5	**0.0**	**13.4**	0.9					
Arctic cod										
Large pelagics	0.6	1.0	**0.0**	**1.4**	0.3	8.7		**4.4**	**13.1**	9.2
Pisci. small pelagics	4.9	8.5	**0.0**	**12.1**	9.2	29.9		**14.9**	**44.8**	24.6
Plank. small pelagics	7.2	12.4	**0.1**	**17.6**	10.6	33.5		**16.8**	**50.3**	32.3
Shrimp	**0.0**	0.0	0.0	0.0	0.0	5.9		**3.0**	**8.9**	7.8
Large crustacea	**0.1**	0.1	0.0	0.2	0.1	**0.4**		0.2	0.6	0.4
Echinoderms										
Molluscs						**0.2**		0.1	0.3	0.2
Polychaetes										
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	**0.1**		0.1	0.2	0.1
Large zooplankton	**0.0**	0.0	0.0	0.0	0.0					
Small zooplankton										
Phytoplankton										
Detritus										
Total	100.0		15.1	229.3	100.0	100.0		50.5	149.5	100.0
TRN	19					15				

Seabirds

Background

In the northern Gulf of St. Lawrence, 64.5% of seabirds are estimated to be found inshore while 35.5% are distributed offshore (Cairns et al. 1991). Inshore seabirds breed in a large number of smaller colonies dispersed along the coastline while offshore species breed in a small number of large colonies (Lack 1967). Major inshore species breeding in the region are the great cormorant (*Phalacrocorax carbo*), double-crested cormorant (*Phalacrocorax auritus*), ring-billed

gull (*Larus delawarensis*), herring gull (*Larus argentatus*), great black-backed gull (*Larus marinus*), common tern (*Sterna hirundo*), Arctic tern (*Sterna paradisaea*), and black guillemot (*Cepphus grylle*). Major offshore species that breed in the region are the northern gannet (*Morus bassanus*), black-legged kittiwake (*Rissa tridactyla*), common murre (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica*), and Leach's storm-petrel (*Oceanodroma leucorhoa*).

Catch/anthropogenic mortality

There are three primary sources of anthropogenic mortality for seabirds in the region: 1) by-catch in fishing gear, 2) hunting, and 3) oil pollution (Montevecchi and Tuck 1987). In the northern Gulf, a few species of seabirds such as ducks and guillemots are hunted for food along Québec's North Shore. Considerable numbers of seabirds (mostly alcids, i.e., murres and puffins, but also others, e.g., gannets) are also caught as by-catch in fishing gear. Bundy et al. (2000) assumed that mortality coming from hunting, by-catch, and maritime traffic amounts to 1×10^{-3} t km^{-2} per year. On the basis of information for seabirds from Newfoundland (NAFO divisions 2J3KL) (Bundy et al. 2000), we estimated a catch rate (1×10^{-3} t km^{-2} yr^{-1} divided by the seabird biomass, 0.012 t km^{-2}) for the Newfoundland ecosystem and we applied it to the divisions 4RS. It totalled 3.35×10^{-4} t km^{-2} yr^{-1} of seabirds being removed annually from the study area through anthropogenic mortality. The inverse solution estimated a catch of 2.28×10^{-4} t km^{-2} yr^{-1}.

Biomass

Unlike the open Atlantic coast of Canada, the Gulf of St. Lawrence is not frequented by large numbers of trans-oceanic and trans-equatorial migrants (Brown 1986). Thus, population estimates based on counts of breeding colonies can be used (Cairns et al. 1990). Data on body mass and population estimates for various seabirds were derived from Chapdelaine (Environment Canada, Migratory Birds Division, Sainte-Foy, Québec, unpublished data). In order to estimate biomass density, we assumed that seabirds were distributed uniformly throughout NAFO divisions 4RST. Consequently, biomass was determined by taking the number of birds multiplied by their respective biomass and divided by the whole 4RST bird inventory area (214,000 km^2) instead of the value usually used for the other groups (the sampling area for divisions 4RS). For species that breed within NAFO divisions 4RST, population estimates (Table 6) were calculated as follows (G. Chapdelaine, unpublished data):

Population estimate = breeders
+ nestlings
+ non-breeders (5)

Population estimate (offshore species) = breeding pairs x 2
+ (0.6 x breeding pairs)
+ (0.8 x breeding pairs) (6)

or

Population estimate (inshore species) = breeding pairs x 2
+ (0.6 x breeding pairs)
+ (1.0 x breeding pairs) (7)

The total biomass estimate for the 4RS study area is 859 t or 0.004 t km^{-2}.

Table 6. Approximate period of occupation, population size, and average body mass and biomass for the main species of seabirds that breed within the study area (NAFO divisions 4RS) or breed primarily or completely outside but occur in the study area or are nestlings. Note that the shaded section indicates inshore seabirds while the unshaded section corresponds to offshore seabirds.

Species	Period of occupation	Population (numbers) of breeders	Population (numbers) of non-breeders and nestlings	Individual mass (kg)	Adjusted average biomass (t)
Great cormorant	Apr-Oct	4,968	3,478	2.25	11.085
Double-crested cormorant	Apr-Oct	78,000	54,600	1.67	205.148
Ring-billed gull	Apr-Oct	66,784	53,427	0.50	35.060
Herring gull	Mar-Dec	95,774	76,619	1.12	160.861
Black-headed gull	Apr-Oct	20	16	0.28	0.006
Great black-backed gull	Mar-Dec	19,472	15,578	1.68	49.068
Common tern	May-Sep	52,536	42,029	0.12	4.729
Caspian tern	May-Sep	22	18	0.61	0.010
Arctic tern	May-Sep	2,010	1,608	0.11	0.166
Black guillemot	Jan-Dec	9,524	6,667	0.40	6.477
Leach's storm-petrel	May-Oct	1,036	725	0.05	0.044
Northern gannet	Apr-Oct	84,248	58,974	3.20	267.333
Black-legged kittiwake	Apr-Oct	16,8752	118,126	0.44	73.628
Common murre	May-Sep	89,320	62,524	0.99	87.685
Thick-billed murre	Apr-Oct	24	17	0.93	0.022
Razorbill	Apr-Oct	16,500	11,550	0.72	11.781
Atlantic puffin	Apr-Oct	48,348	33,844	0.46	22.054
TOTAL	Jan-Dec	651,141	539,790	-	859.176

Production

An energetic model developed for seabirds of the whole Gulf of St. Lawrence (4RST) (G. Chapdelaine, unpublished data) indicates that there are a total of 221,201 nestlings produced each year for all species combined (calculated by assuming that nestlings = number of breeding pairs x

0.6). Multiplying the number of nestlings by the average mass for each species results in a total annual production of 0.0011 t km^{-2} yr^{-1} and a P/B ratio of 0.276 yr^{-1}. The inverse solution estimated a production of 0.0012 t km^{-2} yr^{-1}, representing a P/B of 0.299 yr^{-1}.

Consumption

Estimated food consumption for seabirds in the northern Gulf is 108,419 t yr^{-1} (Chapdelaine, unpublished data). Assuming that consumption is evenly distributed throughout the region results in an estimated annual consumption of 0.507 t km^{-2} yr^{-1}. Based on the previous annual production and the upper GE limit (1%; the value based on the lower GE limit of 0.1% was not realistic), we obtained another consumption estimate of 0.111 t km^{-2} yr^{-1}. This resulted in a mean consumption of 0.309 ± 0.280 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.153 t km^{-2} yr^{-1}, representing a Q/B of 38.165 yr^{-1}.

Diet composition

Seabirds within the study area feed at a variety of trophic levels with most prey being small pelagic fish, benthic invertebrates, and pelagic crustaceans (Cairns et al. 1990). Great cormorants feed mostly on benthic fish, primarily flatfish and cunners (*Tautogolabrus adspersus*), while double-crested cormorants prey heavily on flatfish, sculpins (*Myoxocephalus* sp.), rock gunnels (*Pholis gunnellus*), and sand lance (*Ammodytes* spp.). The only data available from the Gulf of St. Lawrence for black guillemot showed that chicks are fed primarily with benthic fish, particularly sculpins, blennies, and tomcod (*Microgadus tomcod*) (Cairns 1981). Northern gannet, the largest breeding seabird species in the study area, preys on pelagic species such as mackerel and Atlantic saury (*Scomberesox saurus*), but also on sand lance (Burton 1980). Herring gulls, which are the most abundant species in the study area, feed primarily on small pelagic fish and non-marine food (Threlfall 1968; Haycock and Threlfall 1975; Pierroti 1983), but quantitative dietary data from the Gulf are generally lacking for this species as well as for all other gulls, terns, storm-petrels, kittiwakes, and offshore alcids (Cairns et al. 1990). The diets of Arctic tern, recorded on Québec's North Shore (NAFO division 4S; Chapdelaine et al. 1985), as well as the diet of the common tern, the most abundant species in the eastern part of the area (NAFO division 4R), consisted mainly of capelin, sand lance, and pelagic invertebrates. Black-legged kittiwakes are the most abundant species in the western part of the study area (NAFO division 4S) and feed primarily on copepods and euphausiids (Threlfall 1968; Maunder and Threlfall 1972). The final seabird diet was modified following Cairns et al. (1990) and Chapdelaine (unpublished data), who used all available information for the Gulf of St. Lawrence as well as extrapolated information from the closest ecosystems to create a complete diet for all seabird species found in the Gulf of St. Lawrence (north and south, NAFO divisions 4RST). There is no diet data available for Leach's storm-petrel, kittiwakes, murres, razorbills, or Atlantic puffins from the northern Gulf. Information for these species has been extrapolated from Labrador, eastern Newfoundland, and Nova Scotia (Bundy et al. 2000). Based on these different studies, we estimated the resulting diet composition of seabirds used in modelling for the northern Gulf of St. Lawrence (mid-1990s) (Table 7).

Table 7. Diet composition of seabirds used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Seabirds				
Prey	Mean	±SD	Min	Max	Est
Large cod					
Small cod	**0.2**	0.4	0.0	0.5	0.2
Large Green. halibut					
Small Green. halibut	**0.4**	0.6	0.0	0.8	0.4
American plaice	**0.4**	0.6	0.0	0.8	0.4
Flounders	**0.4**	0.6	0.0	0.8	0.4
Skates	**0.4**	0.6	0.0	0.8	0.4
Redfish					
Large demersals					
Small demersals	8.3	10.8	**1.6**	**16.9**	4.4
Capelin	41.0	34.0	**21.9**	**70.0**	62.6
Sand lance	27.9	37.2	**5.0**	**57.6**	5.3
Arctic cod	2.7	4.2	**0.0**	**6.0**	1.7
Large pelagics	**0.0**	0.1	0.0	0.1	0.0
Pisci. small pelagics	9.7	15.1	**0.2**	**21.5**	7.3
Plank. small pelagics	2.2	2.3	**0.8**	**4.0**	3.5
Shrimp	0.6	1.0	**0.0**	**1.4**	1.3
Large crustacea					
Echinoderms					
Molluscs	**0.0**	0.1	0.0	0.1	0.0
Polychaetes					
Other bent. inver.	0.6	1.0	**0.0**	**1.4**	1.4
Large zooplankton	5.0	7.8	**0.0**	**11.1**	10.6
Small zooplankton	**0.2**	0.4	0.0	0.5	0.2
Phytoplankton					
Detritus					
Total	100.0		29.6	194.5	100.0
TRN	17				

Atlantic cod

Background

The northern Gulf cod stock overwinters in the deep waters off south western Newfoundland and then returns to the Gulf, moving northwards off Newfoundland's west coast (NAFO division 4R). Spawning takes place mainly during April and May in Esquiman Channel. During summer, the population migrates to the warmer coastal waters of Québec's lower North Shore and the west coast of Newfoundland.

Commercial landings increased considerably during the late 1950s and 1960s, with the stock declining to low levels by the mid to late 1970s. Following this decline, there was a period of recovery during the early 1980s before the stock collapsed in the early 1990s (Fréchet and Schwab 1998).

For the purpose of this study, Atlantic cod were divided into adults and juveniles, or more accurately, into large and small fish. Smaller fish prey mainly on invertebrates while larger fish feed mainly on fish. These changes tend to occur gradually with increasing length, but here we assumed that the change occurs at 35 cm for cod (Lilly 1991). Northern Gulf cod of age 4+ generally represent fish ≥ 35 cm of length, at which size cod become more piscivorous and begin to recruit to the commercial fishery.

Catch

Landings for cod age 4+ in NAFO divisions 3Pn4RS are available for the 1994–96 period (Fréchet and Schwab 1998). Since cod from these three zones are considered to be part of the same stock, landings from 3Pn were included in the model. The 1994–1996 period modelled here corresponds to the first moratorium (cessation of directed fishing) on cod fishing. There was no directed cod fishery during these years. In the absence of information for this species, it was assumed that there were no discards or by-catch. Mean catch of 4+ cod was $3.26 \times 10^{-3} \pm 1.22 \times 10^{-3}$ t km^{-2} yr^{-1}. Since it was assumed that small cod are not recruited to the fishery, and information on by-catch was not available for the northern Gulf area, catch in the model was set to zero for this group. The inverse solution estimated catch values of 2.87×10^{-3} t km^{-2} yr^{-1} for large cod.

Biomass

The biomass of 4+ cod was based on virtual population analysis estimates of cod biomass at the beginning of the year. The estimated average biomass of 4+ cod was 27,803 t or 0.268 t km^{-2} (SD = 0.008 t km^{-2}). Mean annual biomass for small cod was 3,934 t or 0.038 t km^{-2} (SD = 0.022 t km^{-2}).

Production

P/B of large cod was estimated by catch-curve analysis of groundfish survey data from NAFO divisions 4RS for the 1994–1996 period. The estimate of total mortality ($Z = 0.64\ yr^{-1}$) was determined from the slope of the regression line fitted to the downward side of the catch curve (Sinclair 2001). Since we assume a steady state (no year-to-year change in biomass), total mortality is equal to the P/B ratio ($0.64\ yr^{-1}$) of cod in 1994–1996 (Allen 1971). The annual production estimate was 0.172 ± 0.035 t km^{-2} yr^{-1} (range: 0.138–0.208 t km^{-2} yr^{-1}). Production was also estimated by multiplying biomass by natural mortality (M), plus catch. Natural mortality for large cod was estimated at $0.33\ yr^{-1}$ (Swain and Castonguay 2000). We obtained an annual production of 0.091 ± 0.003 t km^{-2} yr^{-1} (range: 0.075–0.093 t km^{-2} yr^{-1}). Combining the two methods resulted in a mean annual production of 0.113 ± 0.035 t km^{-2} yr^{-1} (range: 0.075–0.208 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.076 t km^{-2} yr^{-1}, resulting in a P/B of $0.28\ yr^{-1}$.

For small cod, production was assumed to be equivalent to biomass multiplied by natural mortality (M), plus catch ([B x M] + C). Natural mortality for small cod was assumed to be 0.6 yr^{-1}, while catch estimates of small cod were assumed to be zero (M. Castonguay, pers. comm.). Using the minimum and maximum biomass values for small cod, we estimated a production range of 0.007 to 0.035 t km^{-2} yr^{-1}, corresponding to an annual production of 0.020 ± 0.016 t km^{-2} yr^{-1}. However, the inverse solution estimated a production of 0.059 t km^{-2} yr^{-1}, representing a P/B value of $1.56\ yr^{-1}$. The production estimate for small cod was higher than the initial upper limit used as a constraint in inverse modelling. This suggested that either biomass or natural mortality (M) was underestimated. If biomass was a good estimate (0.038 t km^{-2}), natural mortality should be equal to $1.56\ yr^{-1}$ to obtain a production of 0.059 t km^{-2} yr^{-1}. If natural mortality ($0.60\ yr^{-1}$) was a good estimate, biomass should be equal to 0.099 t km^{-2} to obtain a production of 0.059 t km^{-2} yr^{-1}.

Consumption

A range of Q/B values was used to estimate the mean Q/B ratio for large cod. These values were based on different studies of food consumption by cod populations of other regions (Palomares and Pauly 1989; Pauly 1989) as well as in the Gulf of St. Lawrence (Waiwood et al. 1980) (Table 8). The Q/B ratios for large cod varied between 1.41 and $4.55\ yr^{-1}$, corresponding to a consumption range between 0.365 and 1.242 t km^{-2} yr^{-1}. Based on the previous mean production (0.113 t km^{-2} yr^{-1}) for large cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.378 and 1.135 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.365 and 1.242 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.803 ± 0.620 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.379 t km^{-2} yr^{-1}, representing a Q/B of $1.42\ yr^{-1}$.

Four studies were used to estimate the mean Q/B ratio for small cod (Daan 1973; Waiwood et al. 1980; Hawkins et al. 1985; Grundwald and Koster 1994). Q/B estimates were extrapolated from food intake measurements (daily or yearly consumption) and body mass or biomass of fish under study. This approach yielded Q/B ratios of $3.250\ yr^{-1}$ (Waiwood et al. 1980), $7.271\ yr^{-1}$ (Daan 1973), $10.730\ yr^{-1}$ (Hawkins et al. 1985), and $2.564\ yr^{-1}$ (Grundwald and Koster 1994). The

Q/B ratios for small cod thus varied between 2.564 and 10.730 yr^{-1}, corresponding to a consumption range between 0.039 and 0.633 t km^{-2} yr^{-1}. Based on the previous mean production (0.020 t km^{-2} yr^{-1}) for small cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.066 and 0.199 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.039 and 0.633 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.336 ± 0.420 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.238 t km^{-2} yr^{-1}, representing a Q/B of 6.279 yr^{-1}.

Table 8. Q/B ratios for Atlantic cod in different regions of the world. Data are from Waiwood et al. (1980)[1], Palomares and Pauly (1989)[2], Pauly (1989)[3], and Froese and Pauly (2002)[4].

Q/B	Region
1.41	North of Norway[3, 4]
1.94	Kattegat, Denmark[3, 4]
2.17	East Baltic Sea[3, 4]
2.19	Georges Bank[3, 4]
2.26	North Sea[2, 3, 4]
2.34	Barents Sea[3, 4]
2.58	West Baltic Sea[2, 3, 4]
3.41	Irish Sea[3, 4]
3.43	Northwest Atlantic[3, 4]
4.08	Iceland[3, 4]
4.36	Faeroe Islands[3, 4]
4.55	Scotland[3, 4]
2.7	West Baltic Sea[2]
2.29	North Sea[2]
1.96	Southern Gulf of St. Lawrence[1]

Diet composition

Stomach content data were available from NAFO divisions 4RS for spring (April-June), summer (July-November), and winter (December-March) from 1993 to 2002 (D. Chabot, unpublished data). We used two periods: (1) 1994–1996, which represents the sampling period of the mid-1990 model; and (2) 1993 and 1997–2002 hereafter termed the "other-years period".

These two periods included spring, summer, and winter samples for large cod. For small cod, 1994–1996 included these three seasons, while the other years included summer samples only. Sampling was length-stratified and covered inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover. To estimate a diet most representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using the product "fullness index x season duration (in months)" as a weighting factor. Empty stomachs were included in the analysis for a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for spring, summer, and winter during the 1994–1996 period were 1137, 4364, and 1510 for large cod and 820, 683, and 708 for small cod, respectively. The

fullness indices, including empty stomachs, were 1.12, 2.10, and 0.24 for spring, summer, and winter in large cod and 4.06, 1.55, and 0.48 in small cod. Sample sizes for spring, summer, and winter during the other-years period were 905, 7409, and 23 for large cod and the fullness indices, including empty stomachs, were 0.25, 1.62, and 0.60. For small cod, sample size for summer during the other-years period was 2659 and the fullness index including empty stomachs was 1.47. These two diets were used as constraints in inverse modelling. Overall, the most important prey items of large cod, in percent mass of stomach content, were capelin, large zooplankton, large crustaceans, and shrimp (72.5% of the diet; Table 9). The most important prey items of small cod were shrimp, capelin, and large zooplankton (89.5%; Table 9).

Table 9. Diet compositions of large and small cod used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large cod (> 35 cm)					Small cod (≤ 35 cm)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	4.3	0.8	**3.8**	**4.8**	3.8	**0.1**	0.1	0.0	0.2	0.1
Large Green. halibut										
Small Green. halibut	**0.4**	0.5	0.0	0.7	0.4	**0.0**	0.0	0.0	0.0	0.0
American plaice	2.3	1.6	**1.1**	**3.4**	3.1	**0.0**	0.0	0.0	0.0	0.0
Flounders	1.1	0.9	**0.5**	**1.7**	0.7	**0.0**	0.0	0.0	0.0	0.0
Skates	**0.0**	0.0	0.0	0.1	0.0					
Redfish	**1.7**	0.55	1.3	2.1	1.7	**0.1**	0.2	0.0	0.3	0.1
Large demersals										
Small demersals	3.3	1.1	**2.4**	**4.1**	2.4	1.6	0.8	**1.0**	**2.2**	1.1
Capelin	34.4	10.8	**26.7**	**42.0**	36.7	30.1	4.8	**26.7**	**33.5**	30.4
Sand lance	4.2	1.3	**3.3**	**5.1**	3.3	4.6	1.2	**3.7**	**5.5**	3.7
Arctic cod	**0.4**	0.3	0.2	0.6	0.4	**0.0**	0.0	0.0	0.0	0.0
Large pelagics										
Pisci. small pelagics	**0.9**	0.1	0.8	1.0	0.9	**0.1**	0.1	0.1	0.1	0.1
Plank. small pelagics	7.2	5.4	**3.4**	**11.0**	5.7	1.2	1.6	**0.0**	**2.3**	0.6
Shrimp	9.4	4.1	**6.5**	**12.2**	9.7	32.8	7.0	**27.9**	**37.7**	31.9
Large crustacea	14.1	11.0	**6.3**	**21.8**	14.8	2.0	0.7	**1.4**	**2.5**	2.0
Echinoderms	**1.1**	0.1	1.0	1.1	1.1	**0.0**	0.0	0.0	0.1	0.0
M[illegible]uscs	**0.4**	0.4	0.1	0.6	0.4	**0.0**	0.0	0.0	0.1	0.0
P[illegible]haetes	**0.1**	0.1	0.1	0.2	0.1	**0.4**	0.2	0.2	0.5	0.4
Other bent. inver.	**0.1**	0.1	0.0	0.2	0.1	**0.0**	0.0	0.0	0.1	0.0
Large zooplankton	**14.6**	0.5	14.3	15.0	14.6	26.6	9.7	**19.8**	**33.5**	29.1
Small zooplankton	**0.2**	0.1	0.1	0.3	0.2	**0.3**	0.3	0.1	0.5	0.3
Phytoplankton										
Detritus										
Total	100.0		72.0	128.0	100.0	100.0		81.0	119.0	100.0
TRN	20					19				

Greenland halibut

Background

Greenland halibut (*Reinhardtius hippoglossoides*) is a deep-water flatfish present in the North Atlantic and North Pacific. In the northwest Atlantic, it is found from Arctic regions to Georges Bank (Bowering 1983). The Gulf of St. Lawrence population is considered to be a small stock, isolated from the main northwest Atlantic stock, completing its entire life cycle within the Gulf (DFO 2002).

Directed fishing for this species with bottom trawls and gillnets developed after the mid–1970s. Landings increased in the 1980s to reach an all-time high in 1987 (11,000 t) but have since declined to around 3,000 t (DFO 2002).

Greenland halibut were divided into large and small fish. Although there is an apparent change in diet composition when fish reach lengths of about 20 cm (Bundy et al., 2000), we separated Greenland halibut into fish larger or smaller than 40 cm, the size at which they are first recruited to the fishery (Brodie 1991). Greenland halibut greater than 40 cm in length are equivalent to fish aged six years and older (Brodie 1991).

Catch

According to the NAFO fisheries statistics, the mean annual landings of large Greenland halibut during the 1994–1996 period were 990 tons or 9.49×10^{-3} t km^{-2} yr^{-1} (SD = 3.88×10^{-3} t km^{-2} yr^{-1}) (Morin and Bernier 1999). The inverse solution estimated a catch of 9.51×10^{-3} t km^{-2} yr^{-1}.

Since it was assumed that small Greenland halibut are not recruited to the fishery, and information on by-catch was not available for the northern Gulf area, catch in the model was set to zero for this group.

Biomass

Annual biomass estimates were obtained from groundfish survey data for the 1994–1996 period. Length-frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software to obtain an estimate of halibut abundance for this zone. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by mean mass at length (derived from length–mass relationships) and summing the results. This resulted in mean biomass estimates for the 1994–96 period of 24,000 t or 0.231 t km^{-2} (SD = 0.108 t km^{-2}) and 21,205 t or 0.204 t km^{-2} (SD = 0.095 t km^{-2}) for large (> 40 cm) and small (≤ 40 cm) Greenland halibut, respectively.

Production

Due to the lack of reliable information on production (P) and total mortality (Z) for this species, it was assumed that production was equivalent to biomass multiplied by natural mortality (M), plus catch. Natural mortality for large Greenland halibut ($M = 0.09\ yr^{-1}$) was estimated using FishBase (Froese and Pauly 2002) and a maximal length of 96.5 cm along with a water temperature of 3°C. When the minimum and maximum biomass values were used, we obtained a production range of 0.024 to 0.040 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.035 t km^{-2} yr^{-1}, representing a P/B of 0.153 yr^{-1}.

For small Greenland halibut, it was assumed that natural mortality was higher (younger fish generally have a higher M than older fish), so a textbook value of 0.6 yr^{-1} was assigned to this group. It was also assumed that there was no catch. When the minimum and maximum biomass values were used, we obtained a production range of 0.062 to 0.188 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.096 t km^{-2} yr^{-1}, representing a P/B of 0.468 yr^{-1}.

Consumption

A Q/B ratio (1.660 yr^{-1}) was estimated using daily food requirements for 6- to 20-year-old Greenland halibut from the northwest Atlantic (Chumakov and Podrazhanskaya 1986). Another Q/B ratio (1.400 yr^{-1}) was calculated using FishBase (Froese and Pauly 2002) for fish at 3°C and having a maximum mass of 9.217 g (B. Morin, Institut Maurice-Lamontagne, personal communication). When the minimum and maximum biomass values and the two previous Q/B ratios were used, we obtained a total consumption of 0.354 t km^{-2} yr^{-1} (range: 0.181–0.572 t km^{-2} yr^{-1}) for large Greenland halibut. Based on the previous mean production (0.030 t km^{-2} yr^{-1}) for large Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.100 and 0.299 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.231 t km^{-2} yr^{-1} instead of 0.100 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.231 and 0.572 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.402 ± 0.241 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.233 t km^{-2} yr^{-1}, representing a Q/B of 1.108 yr^{-1}.

Q/B values for small Greenland halibut were obtained from three different sources. Using the mean daily consumption of 5-year-old Greenland halibut (< 40 cm) (Chumakov and Podrazhanskaya 1986), the Q/B ratio was 4.427 yr^{-1}. The estimate obtained from FishBase (Froese and Pauly 2002), for fish at 3°C with a maximum mass of 586 g (the maximum mass of 40 cm fish from NAFO divisions 4RS; B. Morin, Institut Maurice-Lamontagne, personal communication), was slightly lower, with a Q/B value of 2.500 yr^{-1}. A third estimate (Q/B: 2.665 yr^{-1}) was obtained from a feeding study conducted in West Greenland (Pedersen and Riget 1992a). When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a total consumption of 0.653 t km^{-2} yr^{-1} (range: 0.344–1.388 t km^{-2} yr^{-1}) for small Greenland halibut. Based on the previous mean production (0.107 t km^{-2} yr^{-1}) for small Greenland halibut and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.358 and 1.074 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.344 and 1.388 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.866 ±

0.738 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.412 t km^{-2} yr^{-1}, representing a Q/B of 2.019 yr^{-1}.

Diet composition

Stomach content data for Greenland halibut from NAFO divisions 4RS were available from 1993 to 2002. We used two periods as upper and lower limit constraints in modelling: (1) 1994–1996, which represents the sampling period of the mid-1990 model and also included winter, spring, and summer samples; and (2) 1993 and 1997–2002 hereafter termed the "other-years period", which included spring and summer samples for large Greenland halibut and summer samples only for small Greenland halibut. Sampling was length-stratified and covered inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover. To estimate a diet most representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using the product "fullness index x season duration (in months)" as a weighting factor. Empty stomachs were included in the analysis for a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for spring, summer, and winter, respectively, during the 1994–1996 period were 24, 1344, and 45 for large Greenland halibut and 30, 2446, and 25 for small Greenland halibut. The fullness indices, including empty stomachs, were 0.38, 0.37, and 1.20 for spring, summer, and winter in large Greenland halibut and 2.31, 0.68, and 1.01 in small Greenland halibut. Sample sizes for spring and summer during the other-years period were 593 and 1881 for large Greenland halibut and the fullness indices, including empty stomachs, were 0.12 and 0.37, respectively. For small Greenland halibut, sample size for summer during the other-years period was 5023 and the fullness index including empty stomachs was 0.54.

These two diets were used as constraints in inverse modelling (Table 10). The most important prey items of large Greenland halibut were capelin, shrimp, small planktivorous pelagics, and small demersals (90.2% of the diet; Table 10). The most important prey items of small Greenland halibut were capelin, shrimp, and large zooplankton (90.2%; Table 10).

Table 10. Diet compositions of large and small Greenland halibut used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large Greenland halibut (> 40 cm)					Small Greenland halibut (≤ 40 cm)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	0.6	0.9	**0.0**	**1.3**	0.1	**0.1**	0.2	0.0	0.3	0.1
Large Green. halibut										
Small Green. halibut	0.5	0.7	**0.1**	**1.0**	1.0	**0.1**	0.2	0.0	0.3	0.1
American plaice	**0.0**	0.0	0.0	0.1	0.0					
Flounders	**0.3**	0.3	0.1	0.5	0.3	**0.1**	0.2	0.0	0.3	0.0
Skates	**0.1**	0.1	0.0	0.2	0.1					
Redfish	5.0	6.8	**0.2**	**9.9**	9.8	**0.4**	0.5	0.0	0.8	0.4
Large demersals										
Small demersals	15.9	12.4	**7.2**	**24.7**	8.1	6.5	5.9	**2.3**	**10.6**	2.3
Capelin	32.7	2.0	**31.3**	**34.1**	32.8	57.2	29.8	**36.1**	**78.3**	59.9
Sand lance	**0.0**	0.0	0.0	0.0	0.0	**0.4**	0.58	0.0	0.8	0.4
Arctic cod	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Large pelagics	**0.0**	0.0	0.0	0.0	0.0					
Pisci. small pelagics	1.6	1.6	**0.5**	**2.7**	1.0	2.0	1.3	**1.1**	**2.9**	1.1
Plank. small pelagics	16.6	12.6	7.7	**25.5**	22.3	**0.0**	0.0	0.0	0.0	0.0
Shrimp	25.0	6.6	**20.3**	**29.7**	22.7	18.6	13.1	**9.3**	**27.9**	18.9
Large crustacea	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Echinoderms	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Molluscs	**0.0**	0.0	0.0	0.0	0.0	**0.1**	0.1	0.0	0.2	0.1
Polychaetes	**0.0**	0.0	0.0	0.1	0.0	**0.0**	0.0	0.0	0.0	0.0
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.0	0.0	0.0	0.0
Large zooplankton	1.4	0.65	**0.9**	**1.9**	1.5	14.4	10.2	**7.2**	**21.6**	16.6
Small zooplankton	**0.0**	0.0	0.0	0.0	0.0	**0.0**	0.1	0.0	0.1	0.0
Phytoplankton										
Detritus										
Total	100.0		68.3	131.7	100.0	100.0		56.1	143.9	100.0
TRN	21					18				

American plaice, flounders, and skates

Background

All flatfish other than Greenland halibut were divided into three groups: American plaice (*Hippoglossoides platessoides*), flounders, and skates.

American plaice is widely distributed throughout the northwest Atlantic (from west Greenland to the Gulf of Maine) and is usually found at intermediate depths (80–250 m) (Morin et al. 1998). It has been exploited in NAFO divisions 4RS since 1947, with commercial catches peaking in 1977. Annual catches then began to fall until the mid-1980s, when they levelled off at around 2,000 t, but yearly landings have since declined to around 1,000 t.

The flounder group consisted of witch flounder (*Glyptocephalus cynoglossus*), yellowtail flounder (*Limanda ferruginea*), fourspot flounder (*Paralichthys oblongus*), and winter flounder (*Pseudopleuronectes americanus*). Flounders were grouped together on the basis of their similar feeding behaviour. These four species are sedentary bottom-dwelling flatfish that live in relatively deep water, except for winter flounder, which lives mostly in infra-littoral waters. Their distribution ranges from the coast of Labrador in the north to North Carolina in the south. Since the 1950s, important commercial catches have occurred in the deep waters bordering the Laurentian Channel. A long-standing fishery has also been in place in shallower waters for winter flounder. The key species of the flounder group is witch flounder, mainly because of its high biomass and commercial significance, but also because there were no captures of the other species by the research surveys, which indicates that their biomass was quite low. These other species are occasionally found in the stomachs of certain predators (e.g., seals).

The skate group included two species: the thorny skate (*Amblyraja radiata*), considered here as the key species for the group, and the smooth skate (*Malacoraja senta*). The thorny skate is widely distributed throughout the North Atlantic. The greatest concentrations are generally found in the higher part of continental shelves, at depths greater than 110 m (McEachran et al. 1976). The smooth skate is found throughout the northwest Atlantic, from the Gulf of St. Lawrence to Georges Bank (Scott and Scott 1988). Surveys conducted since the 1940s have shown that the greatest concentrations are found in the Gulf of St. Lawrence, on the Grand Banks, and on the Scotian Shelf. This species lives at depths of 50 to 700 m but is mostly caught between 90 and 325 m (McKone and LeGrow 1983). Fishing activity is less important for the smooth skate than for the thorny skate.

Catch

According to the landing statistics (NAFO 1999), mean annual landings during the 1994–1996 period in NAFO divisions 4RS were $1.78 \times 10^{-3} \pm 6.46 \times 10^{-4}$ t km^{-2} yr^{-1} for American plaice, $1.62 \times 10^{-3} \pm 3.45 \times 10^{-4}$ t km^{-2} yr^{-1} for witch flounder, and $1.11 \times 10^{-3} \pm 2.96 \times 10^{-4}$ t km^{-2} yr^{-1} for skates. The inverse solution estimated catch values of 1.88×10^{-2}, 1.63×10^{-3}, and 1.09×10^{-3} t km^{-2} yr^{-1} for American plaice, flounders, and skates, respectively.

Biomass

Annual biomass estimates for the three groups were obtained using *PACES* to analyze research survey data from NAFO divisions 4RS during the 1994–96 period. For flounders, mean biomass comprised witch flounder biomass, the only species for which data were available from the study area. Skate biomass was made up of both thorny and smooth skates. Mean biomass in NAFO divisions 4RS during the 1994–1996 period was estimated at 100,035 t or 0.964 t km^{-2} (SD = 0.216 t km^{-2}) for American plaice, 6,605 t or 0.064 t km^{-2} (SD = 0.029 t km^{-2}) for flounders, and 16,672 t or 0.161 t km^{-2} (SD = 0.016 t km^{-2}) for skates.

Production

There was no information available on production or total mortality (Z) of American plaice, flounders, or skates within the study area. It was therefore assumed that for each group, production is equivalent to biomass multiplied by natural mortality (M), plus the catch. Natural mortality was assumed to be 0.220 yr^{-1} for American plaice (Pitt 1982) and 0.214 yr^{-1} for skates (Simon and Frank 1996). Due to a lack of information, natural mortality of flounders was assumed to be 0.200 yr^{-1}. When the minimum and maximum biomass values were used for each group, we obtained production ranges of 0.142 to 0.244 t km^{-2} yr^{-1} for American plaice, 0.009 to 0.020 t km^{-2} yr^{-1} for flounders, and 0.030 to 0.039 t km^{-2} yr^{-1} for skates. Production values estimated by the inverse solution were 0.220 t km^{-2} yr^{-1} (P/B = 0.228 yr^{-1}) for American plaice, 0.020 t km^{-2} yr^{-1} (P/B = 0.309 yr^{-1}) for flounders, and 0.039 t km^{-2} yr^{-1} (P/B = 0.241 yr^{-1}) for skates.

Consumption

Consumption estimates for these three groups were derived from different sources. For all three groups, FishBase provided an initial Q/B estimate based on fish at 3°C (Froese and Pauly 2002). The Q/B values obtained in this way were 2.2 yr^{-1} for American plaice, 2.4 yr^{-1} for flounders (this value was the only one available for the group), and 1.5 yr^{-1} for skates.

For American plaice, a second estimate of consumption was derived from daily ration data using the model of Elliott and Persson (1978) with fish from the Grand Banks of Newfoundland (Zamarro 1992). Mean daily consumption, calculated monthly, were 0.04% to 0.64% of body mass per day, with a final mean of 0.34%. Accordingly, the mean annual Q/B ratio was 1.241 yr^{-1}. A third study, with fish from Passamaquody Bay (New Brunswick), was used to determine consumption for American plaice (MacDonald and Waiwood 1987). The authors estimated food consumption to be 1.28% of body mass per day, resulting in a Q/B ratio of 4.672 yr^{-1} (assuming that feeding is constant throughout the year). When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a total consumption of 2.606 t km^{-2} yr^{-1} (range: 0.887–5.129 t km^{-2} yr^{-1}) for American plaice. Based on the previous mean production (0.203 t km^{-2} yr^{-1}) for American plaice and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.676 and 2.029 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.964 t km^{-2} yr^{-1} instead of

0.676 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.964 and 5.129 t km^{-2} yr^{-1}, corresponding to a mean consumption of 3.046 ± 2.945 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.059 t km^{-2} yr^{-1} for American plaice, representing a Q/B of 1.099 yr^{-1}.

For the flounder group, the only available value was obtained from FishBase as described above. When the minimum and maximum biomass values were used, this resulted in a total consumption range of 0.087 to 0.225 t km^{-2} yr^{-1}. However, based on the previous mean production (0.014 t km^{-2} yr^{-1}) for flounders and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 0.046 and 0.137 t km^{-2} yr^{-1}, respectively. However, assuming that these species would eat at least as much food as their biomass (Q/B ≥ 1), we used 0.064 t km^{-2} yr^{-1} instead of 0.046 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.064 and 0.225 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.144 ± 0.114 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.083 t km^{-2} yr^{-1} for flounders, representing a Q/B of 1.302 yr^{-1}.

For skates, two other estimates of the Q/B ratio were taken into account. The first of these was determined for thorny skates from the Barents Sea (Dolgov 1997). Estimated annual consumption from this study was divided by mean biomass, resulting in an annual Q/B ratio 2.369 yr^{-1} for our study area. The other estimate, based on thorny skate stomachs collected in the North Sea (Vinter 1989), produced a Q/B ratio of 2.865 yr^{-1} for our study area. When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a total consumption of 0.360 t km^{-2} yr^{-1} (range: 0.225–0.511 t km^{-2} yr^{-1}) for skates. Based on the previous mean production (0.034 t km^{-2} yr^{-1}) for skates and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.113 and 0.338 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass (Q/B ≥ 1), we used 0.161 t km^{-2} yr^{-1} instead of 0.113 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were thus 0.161 and 0.511 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.336 ± 0.248 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.198 t km^{-2} yr^{-1} for skates, representing a Q/B of 1.232 yr^{-1}.

Diet composition

Diet data from NAFO divisions 4RS during the 1994–1996 period were unavailable for all three groups, so studies from other areas and time periods were used instead. For American plaice, two studies provided some information on diet composition. In the first study, of 180 food-containing stomachs collected from bottom trawl surveys in western Nova Scotia from 1969 to 1972, primary prey items were echinoderms (60.4%) and large crustaceans (18.8%) (Langton and Bowman 1980). In the second study, based on 338 food-containing stomachs collected from the Flemish Cap bank during the summer of 1993, benthic species were the most important prey, including echinoderms (principally brittle stars; 86.4% by volume), large zooplankton such as hyperiids (10.9% by volume), and shrimp (1.0% by volume) (Rodriguez-Marin et al. 1994).

For flounders, very little diet information was available. The summer diet of witch flounder on Flemish Cap was used and is principally made up of polychaetes (80.2% by volume), other benthic invertebrates (8.4% by volume), echinoderms (5.7% by volume), and bivalves (4.6% by volume) (Rodriguez-Marin et al. 1994).

The diet of the thorny skate was assumed to be representative of the entire skate group. Templeman (1982) examined the annual diet of thorny skates from the northwest Atlantic and found that the main prey species were (by volume) small demersal feeders (25.5%), redfish (23.6%), sand lance (15.8%), large crustaceans (14.3%), and small Atlantic cod (5.7%). A second study from the same area examined the diet composition of thorny skate from April 1969 to April 1970 (McEachran et al. 1976). Fish such as redfish, flounders, skates, small demersal feeders, and sand lance (each amounting to 10%), as well as invertebrates such as polychaetes (23.0%) and large crustaceans (18.9%) were the most important prey (by volume) in that skate diet.

Due to the uncertainties with diet data, we also used the diet compositions for these three groups found by Bundy et al. (2000) in the Newfoundland–Labrador Shelf and Savenkoff et al. (2004) in the southern Gulf of St. Lawrence (mid-1990s) to construct the upper and lower limits used to constrain values in inverse modelling (Table 11).

Table 11. Diet compositions of American plaice, flounders, and skates used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	American plaice					Flounders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.1**	0.3	0.0	0.5	0.1					
Large Green. halibut										
Small Green. halibut	**0.2**	0.5	0.0	0.8	0.2					
American plaice	0.5	1.5	**0.0**	**2.1**	0.7					
Flounders	0.2	0.6	**0.0**	**0.9**	0.0					
Skates										
Redfish	**0.0**	0.0	0.0	0.0	0.0					
Large demersals										
Small demersals	0.6	1.8	**0.0**	**2.5**	0.0	1.8	3.2	**0.0**	**4.6**	1.1
Capelin	9.1	24.8	**0.0**	**35.1**	4.1	1.8	3.3	**0.0**	**4.7**	2.1
Sand lance	3.9	10.7	**0.0**	**15.1**	0.0	1.9	3.4	**0.0**	**4.9**	0.2
Arctic cod	**0.1**	0.1	0.0	0.2	0.1					
Large pelagics										
Pisci. small pelagics	**0.0**	0.0	0.0	0.0	0.0					
Plank. small pelagics	**0.0**	0.0	0.0	0.1	0.0	1.1	2.0	**0.0**	**2.9**	0.9
Shrimp	3.5	9.7	**0.0**	**13.7**	0.0	1.0	1.8	**0.0**	**2.6**	1.3
Large crustacea	4.8	13.3	**0.0**	**18.8**	0.5	0.9	1.6	**0.0**	**2.2**	1.4
Echinoderms	22.3	61.1	**0.0**	**86.4**	9.2	15.2	26.9	**0.4**	**38.4**	9.0
Molluscs	13.2	36.3	**0.0**	**51.4**	34.0	15.9	28.7	**0.0**	**40.6**	11.0
Polychaetes	5.0	13.7	**0.0**	**19.4**	12.8	34.6	50.8	**8.2**	**80.1**	42.3
Other bent. inver.	9.9	27.2	**0.0**	**38.5**	33.0	22.1	28.9	**7.9**	**48.7**	27.0
Large zooplankton	26.1	68.4	**2.3**	**99.1**	5.0	2.0	3.6	**0.0**	**5.1**	2.0
Small zooplankton	0.3	0.8	**0.0**	**1.1**	0.2	**0.0**	0.1	0.0	0.1	0.0
Phytoplankton										
Detritus						1.6	2.9	**0.0**	**4.1**	1.8
Total	100.0		2.3	385.5	100.0	100.0		16.5	239.0	100.0
TRN	19					13				

Table 11. Cont.

	Skates				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod	2.1	4.4	**0.0**	**6.2**	0.5
Large Green. halibut					
Small Green. halibut	**0.1**	0.1	0.0	0.2	0.1
American plaice	**0.1**	0.1	0.0	0.2	0.1
Flounders	3.4	7.1	**0.0**	**10.0**	0.2
Skates	3.4	7.1	**0.0**	**10.0**	2.5
Redfish	8.0	16.7	**0.0**	**23.6**	18.0
Large demersals					
Small demersals	12.9	23.3	**2.6**	**35.5**	2.6
Capelin	3.4	7.1	**0.0**	**10.0**	8.5
Sand lance	6.2	12.8	**0.0**	**18.2**	0.1
Arctic cod	**0.1**	0.1	0.0	0.2	0.1
Large pelagics					
Pisci. small pelagics	2.5	5.1	**0.0**	**7.2**	1.2
Plank. small pelagics	27.6	57.6	**0.0**	**81.4**	15.6
Shrimp	3.2	5.5	**0.8**	**8.6**	5.0
Large crustacea	15.7	26.5	**4.4**	**41.9**	21.6
Echinoderms	0.7	1.4	**0.0**	**2.0**	1.6
Molluscs	0.7	1.3	**0.2**	**2.0**	1.6
Polychaetes	9.0	13.8	**3.5**	**23.0**	18.2
Other bent. inver.	0.4	0.9	**0.0**	**1.3**	1.2
Large zooplankton	0.7	1.4	**0.0**	**2.0**	1.3
Small zooplankton	**0.0**	0.1	0.0	0.1	0.0
Phytoplankton					
Detritus					
Total	100.0		11.5	283.5	100.0
TRN	20				

Redfish and demersal feeders

Background

The demersal feeders represent deep-water demersal species from NAFO divisions 4RS. Because of its economic and ecological importance in the system, redfish was treated separately while the remaining demersal species were divided into large and small demersal feeders.

Redfish distribution in the northwest Atlantic ranges from west Greenland to the Gulf of Maine (Atkinson and Melteff 1987). Two redfish species are known to be the main component of

the northwest Atlantic stock: *Sebastes mentella*, which generally occupies waters deeper than 250 m, and *S. fasciatus*, usually found in shallower waters down to 300 m. Redfish usually inhabit waters from 100 to 700 m in depth and are ovoviviparous. Mating usually occurs in September or October, and females release live young from April to July. Redfish grow quite slowly, generally taking 8 to 10 years before being recruited to the commercial fishery at approximately 25 cm in length. These species have been commercially fished since the early 1950s, but a moratorium was imposed on redfish fishing in 1995.

The large demersal feeder group is mainly made up of white hake (*Urophycis tenuis*), black dogfish (*Centroscyllium fabricii*), marlin spike grenadier (*Nezumia bairdi*), Atlantic halibut (*Hippoglossus hippoglossus*), wolffish (*Anarhichas* spp.), common lumpfish (*Cyclopterus lumpus*), haddock (*Melanogrammus aeglefinus*), longfin hake (*Urophycis chesteri*), large eelpout (Zoarcidae), monkfish (*Lophius americanus*), and grenadiers (Macrouridae). Information was very limited for most of these species in NAFO divisions 4RS.

The small demersal feeders group includes sculpins (Cottidae), small eelpouts (Zoarcidae), fourbeard rockling (*Enchelyopus cimbrius*), cunners (*Tautogolabrus adspersus*), gunnels (Pholidae), lumpsuckers (*Eumicrotremus* sp.), and blennies (Stichaeidae). Juvenile large demersal were also considered as small demersal feeders. Unfortunately, little is known about these species and only scant information from the study area was available.

Catch

Total landings for redfish and the large demersal feeder group in NAFO divisions 4RS during the 1994–96 period were calculated by summing the NAFO landing statistics for each of the species listed above (NAFO 1999). Since there is no fishery for species in the small demersal feeder group and by–catch information was unavailable, catch was set at zero for this group. For redfish, the average annual landings were 1,731 t or 1.67×10^{-2} t km^{-2} yr^{-1} (SD = 4.00×10^{-2} t km^{-2} yr^{-1}). For the large demersal feeders, Atlantic halibut, haddock, and monkfish were the main species caught in 4RS during the 1994–96 period (95% of total landings). The average annual catch of the large demersal feeders was estimated at 184 t or 1.78×10^{-3} t km^{-2} yr^{-1} (SD = 1.12×10^{-3} t km^{-2} yr^{-1}). The inverse solution estimated catch values of 2.16×10^{-2} and 1.79×10^{-3} t km^{-2} yr^{-1} for redfish and large demersal feeders, respectively.

Biomass

The *Needler* scientific survey provided data from NAFO divisions 4RS during the 1994–96 period to estimate annual biomass. For redfish, length frequency data from each year were extrapolated to the whole northern Gulf area using the *PACES* software. Total biomass was estimated each year by multiplying the abundance estimate for each length increment by the mean mass-at-length (derived from length–mass relationships) and summing the results. For the large demersal feeder group, total biomass in the study area for each species was directly computed with *PACES* and results were summed. Average annual biomass estimates were 148,682 t or 1.432 t km^{-2} (SD = 0.623 t km^{-2}) for redfish and 18,263 t or 0.176 t km^{-2} (SD = 0.030 t km^{-2}) for large demersal feeders.

Biomass for the small demersal feeder group was determined in the same way as for their large counterparts. Average annual biomass was estimated at 4.358 t or 0.042 t km^{-2} (SD = 0.011 t km^{-2}) for the entire study area during the 1994–96 period. However, based on initial inverse modelling runs and due to the large uncertainty related to the biomass of this group, the previous value seemed to be too low to meet predator demands and was used as a lower limit. The upper limit was set to the third of the mean value (1.343 t km^{-2}) used by Morissette et al. (2003) in the northern Gulf of St. Lawrence during the mid-1980s. A mean biomass of 0.241 ± 0.292 t km^{-2} was used here.

Production

Information on production and total mortality (Z) of redfish and large demersal species is lacking. Production was therefore assumed to be equivalent to biomass multiplied by natural mortality (M), plus the catch (Allen 1971). Natural mortality (M) was assumed to be 0.125 yr^{-1} for redfish and 0.130 yr^{-1} for large demersal feeders. The lower value for large demersal feeders was chosen because this group contains species such as black dogfish and Atlantic halibut that are slow growing, long lived, and have relatively low natural mortality rates. When the minimum and maximum biomass values were used for each group, we obtained production ranges of 0.124 to 0.318 t km^{-2} yr^{-1} for redfish and 0.019 to 0.027 t km^{-2} yr^{-1} for large demersal feeders. Production values estimated by the inverse solution were 0.250 t km^{-2} yr^{-1} (P/B = 0.174 yr^{-1}) for redfish and 0.040 t km^{-2} yr^{-1} (P/B = 0.227 yr^{-1}) for large demersal feeders. The production estimate for large demersal feeders was higher than the initial upper limit used as the constraint in inverse modelling. This suggested that either biomass or natural mortality for large demersal feeders was underestimated. If biomass (0.176 t km^{-2}) was properly estimated, then natural mortality should be equal to 0.22 yr^{-1} to obtain a production of 0.040 t km^{-2} yr^{-1}. But if natural mortality (0.130 yr^{-1}) was properly estimated, then biomass should be equal to 0.294 t km^{-2} to obtain a production of 0.040 t km^{-2} yr^{-1}.

The same methodology was used for the small demersal feeders. Natural mortality was set to 0.250 yr^{-1}, the value estimated by FishBase for fourbeard rockling (the key species for the group) at a temperature of 3°C (Froese and Pauly 2002). When the minimum and maximum biomass values were used, we obtained a production range of 0.009 to 0.112 t km^{-2} yr^{-1}. The production value estimated by the inverse solution was 0.092 t km^{-2} yr^{-1} (P/B = 0.384 yr^{-1}) for small demersal feeders.

Consumption

FishBase was used to estimate the Q/B ratio of both redfish and large demersal feeders, assuming a water temperature of 3°C (Froese and Pauly 2002). This resulted in Q/B ratios of 2.1 and 3.1 yr^{-1}, respectively, for redfish and the large demersal feeders.

Other information on redfish consumption is available. Dolgov and Revetnyak (1990) estimated annual food consumption to biomass ratios for Barents Sea deep-water redfish (*Sebastes mentella*) that varied from a high of 6.0 yr^{-1} for fingerlings down to around 1.3 yr^{-1} for fish of 19 years of age. Since fingerlings and very young fish did not make up a significant part of

the biomass, the mean Q/B of fish from 10 to 19 years of age was computed. This produced a mean Q/B ratio of 1.490 yr^{-1}. In another study on redfish from west Greenland, it was determined that daily rations were 0.46% and 0.86% of body mass for the autumn–winter and spring–summer periods, respectively (Pedersen and Riget 1992b). These two values were averaged, which gave a mean of 0.66% body mass per day and was equivalent to a Q/B ratio of 2.409 yr^{-1}. On Georges Bank, the Q/B ratio for redfish was estimated at 7.970 yr^{-1} (Pauly 1989). When the minimum and maximum biomass values and the four previous Q/B ratios were used, we obtained a total consumption of 5.002 t km^{-2} yr^{-1} (range: 1.566–17.145 t km^{-2} yr^{-1}) for redfish. Based on the previous mean production (0.190 t km^{-2} yr^{-1}) for redfish and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.634 and 1.903 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 1.432 t km^{-2} yr^{-1} instead of 0.634 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 1.432 and 17.145 t km^{-2} yr^{-1}, corresponding to a mean consumption of 9.288 ± 11.110 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.484 t km^{-2} yr^{-1} for redfish, representing a Q/B of 1.036 yr^{-1}.

For the large demersal feeders, the only available value was obtained from FishBase as described above. When the minimum and maximum biomass values were used, this resulted in a total consumption of 0.545 t km^{-2} yr^{-1} (range: 0.437–0.604 t km^{-2} yr^{-1}) for the large demersal feeders. Based on the previous mean production (0.024 t km^{-2} yr^{-1}) for large demersal feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.079 and 0.237 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.176 t km^{-2} yr^{-1} instead of 0.079 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.176 and 0.604 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.390 ± 0.303 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.257 t km^{-2} yr^{-1} for large demersal feeders, representing a Q/B of 1.461 yr^{-1} (if initial biomass was not underestimated).

The only information available for the small demersal feeders were Q/B estimates computed from FishBase (Froese and Pauly 2002). We averaged the Q/B ratios obtained in this way for the two most abundant species of the group, fourbeard rockling (2.70 yr^{-1}) and Atlantic soft pout (4.30 yr^{-1}). When the minimum and maximum biomass values were used, this resulted in a total consumption of 0.843 t km^{-2} yr^{-1} (range: 0.093–1.924 t km^{-2} yr^{-1}) for the small demersal feeders. Based on the previous mean production (0.060 t km^{-2} yr^{-1}) for small demersal feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.201 and 0.602 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.241 t km^{-2} yr^{-1} as lower limit. The resulting lower and upper consumption limits were 0.241 and 1.924 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.083 ± 1.190 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.402 t km^{-2} yr^{-1} for small demersal feeders, representing a Q/B of 1.670 yr^{-1}.

Diet composition

Stomach content data for redfish were available from 1993 to 1999. We used two periods: (1) 1994–1996, which represented the sampling period of the mid-1990 model and included winter, spring, and summer samples, and (2) 1993 and 1997–1999 hereafter termed the "other-

years period" which included spring and summer samples. Sampling was length-stratified and covered inshore and offshore zones for all seasons. In winter, inshore sampling was reduced due to ice cover. To estimate a diet most representative of the entire year, average diets were calculated for each season (in % mass) and then averaged into a final diet using sample size as a weighting factor. Empty stomachs were included in the analysis for a better estimate of seasonal fluctuations in stomach fullness. Sample sizes for spring, summer, and winter, respectively, during the 1994–1996 period were 369, 1001, and 159. The fullness indices, including empty stomachs, were 0.37, 0.54, and 0.96 for spring, summer, and winter, respectively. Sample sizes for spring and summer during the other-years period were 294 and 1493, and the fullness indices, including empty stomachs, were 0.04 and 0.58, respectively. The most important prey items of redfish were shrimp, large zooplankton, and capelin for the 1994–1996 (94.2% of the diet) and other-years (97.2% of the diet) periods. The redfish diet from Bundy et al. (2000), in which main prey items were large zooplankton (53.8%), small zooplankton (16.1%), and small planktivorous pelagics (24.5%), was also used. The final diet compositions are shown in Table 12.

For large demersal feeders, diet was assumed to be that of white hake, the key species of the group. There was no diet information available for the Gulf of St. Lawrence, but some was found for the northeast United States and Scotian Shelf (Langton and Bowman 1980). In 169 white hake stomachs from these areas, small piscivorous pelagic feeders, small demersal feeders, and small planktivorous pelagic feeders were the most important prey items. We also used the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Savenkoff et al. (2004) for the southern Gulf of St. Lawrence (mid-1990s) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 12).

There was no information found on the diet of small demersal feeders. So, we used the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Savenkoff et al. (2004) for the southern Gulf of St. Lawrence (mid-1990s) to construct the upper and lower limits used as constraints in inverse modelling for this group (Table 12).

Table 12. Diet compositions of redfish, large demersal feeders, and small demersal feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Redfish					Large demersal feeders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	**0.1**	0.1	0.0	0.2	0.1	1.7	4.7	**0.0**	**6.6**	0.5
Large Green. halibut										
Small Green. halibut						**0.2**	0.5	0.0	0.7	0.2
American plaice						0.4	1.2	**0.0**	**1.7**	1.0
Flounders						0.3	0.7	**0.0**	**1.1**	0.0
Skates						2.4	6.7	**0.0**	**9.4**	0.8
Redfish	1.1	1.7	**0.0**	**2.4**	1.9	1.2	3.4	**0.0**	**4.8**	2.8
Large demersals										
Small demersals	0.9	1.3	**0.1**	**1.9**	0.1	5.0	13.7	**0.1**	**19.5**	0.1
Capelin	10.3	14.4	**0.7**	**21.1**	20.8	2.4	6.7	**0.0**	**9.4**	4.8
Sand lance	0.7	1.0	**0.0**	**1.4**	0.0	2.4	6.7	**0.0**	**9.4**	0.0
Arctic cod						1.7	4.7	**0.0**	**6.6**	0.2
Large pelagics										
Pisci. small pelagics	**0.3**	0.4	0.0	0.5	0.3	4.1	11.5	**0.0**	**16.2**	0.0
Plank. small pelagics	11.5	17.3	**0.0**	**24.5**	0.7	22.4	61.8	**0.0**	**87.4**	0.0
Shrimp	31.1	41.7	**3.5**	**62.4**	6.2	7.3	20.2	**0.0**	**28.6**	3.1
Large crustacea						18.2	50.3	**0.1**	**71.3**	1.4
Echinoderms						5.1	14.1	**0.0**	**19.9**	9.8
Molluscs	**0.0**	0.0	0.0	0.0	0.0	1.7	4.7	**0.0**	**6.7**	5.4
Polychaetes	**0.0**	0.0	0.0	0.0	0.0	14.7	40.8	**0.0**	**57.7**	47.4
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	3.6	9.9	**0.0**	**14.1**	10.6
Large zooplankton	36.3	21.7	**23.1**	**53.8**	53.8	4.7	13.1	**0.0**	**18.5**	11.1
Small zooplankton	7.8	11.1	**0.4**	**16.1**	16.1	0.4	1.0	**0.0**	**1.4**	1.0
Phytoplankton										
Detritus										
Total	100.0		27.8	184.3	100.0	100.0		0.2	391.0	100.0
TRN	13					20				

Table 12. Cont.

	Small demersal feeders				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod	4.6	10.3	**0.0**	**14.6**	0.5
Large Green. halibut					
Small Green. halibut					
American plaice	9.2	20.6	**0.0**	**29.1**	13.4
Flounders	6.6	14.8	**0.0**	**20.9**	0.0
Skates					
Redfish					
Large demersals					
Small demersals	10.2	21.5	**1.0**	**31.4**	1.0
Capelin	0.6	1.4	**0.0**	**2.0**	1.1
Sand lance	0.3	0.7	**0.0**	**1.0**	0.0
Arctic cod	**0.2**	0.4	0.0	0.5	0.2
Large pelagics					
Pisci. small pelagics	**0.1**	0.1	0.0	0.2	0.1
Plank. small pelagics	2.8	6.3	**0.0**	**8.9**	0.0
Shrimp	6.8	12.8	**1.7**	**19.9**	4.9
Large crustacea	26.0	57.4	**0.5**	**81.6**	5.1
Echinoderms	3.2	7.1	**0.0**	**10.0**	5.3
Molluscs	3.2	7.1	**0.0**	**10.0**	7.2
Polychaetes	6.3	14.1	**0.0**	**20.0**	19.3
Other bent. inver.	13.3	29.7	**0.0**	**42.0**	34.0
Large zooplankton	5.0	11.1	**0.0**	**15.7**	4.6
Small zooplankton	1.6	3.5	**0.0**	**5.0**	3.3
Phytoplankton					
Detritus					
Total	100.0		3.3	312.7	100.0
TRN	17				

Forage fish

Background

There was very little information available on forage fish from NAFO divisions 4RS. In most cases, data from other areas were used for the model. Four species were identified and separated into the following groups: capelin (*Mallotus villosus*), sand lance (*Ammodytes dubius* and *A. americanus*), and Arctic cod (*Boreogadus saida*).

Capelin is a small, short-lived pelagic fish that spends most of its life offshore, moving inshore only to spawn. The species is exploited commercially in some areas and is probably the most important forage fish of the northern Gulf of St. Lawrence.

Sand lance are small planktivorous semi-demersal fish found off the northwest Atlantic coast from Greenland to North Carolina (Nizinski et al. 1990). The northern sand lance (*Ammodytes dubius*) lives at water depths greater than 80 m, where water is colder, approximately 1°C. American sand lance (*Ammodytes americanus*) lives generally at depths of less than 20 m with temperatures around 6°C. Since the nearshore region (depths < 37 m) was not included in the model, the northern sand lance should be the most abundant species.

The Arctic cod has a circumpolar distribution and is found in the northwest Atlantic from arctic waters in the north down to the southern Gulf of St. Lawrence (Scott and Scott 1988). This species is pelagic and feeds mainly on invertebrates found in the upper part of the water column. Arctic cod is a key component of the marine food web of arctic waters (Hop et al. 1997) and an important link in the transfer of energy from zooplankton to other fish, marine mammals, and seabirds (Lilly et al. 1994).

Catch

For capelin and sand lance, the average annual landings for the 1994–96 period in the study area were estimated from NAFO landing statistics to be 2,536 t ($2.45 \times 10^{-2} \pm 4.97 \times 10^{-2}$ t km^{-2} yr^{-1}) and 2 t ($6.42 \times 10^{-6} \pm 1.11 \times 10^{-5}$ t km^{-2} yr^{-1}), respectively (NAFO 1999). The inverse solution estimated catch values of 3.42×10^{-2} and 5.80×10^{-6} t km^{-2} yr^{-1} for capelin and sand lance, respectively. There was no catch data entered in the model for Arctic cod.

Biomass

Annual biomass estimates of capelin were obtained from the *Needler* scientific surveys for the 1994–96 period using the *PACES* software. This resulted in a mean annual biomass estimate of 45,320,090 t or 436.559 t km^{-2} for the 4RS ecosystem (range: 173.672–802.777 t km^{-2}). Since the biomass of this group was a gross approximation, we also used an estimate (0.070 t km^{-2}) from acoustic surveys in the Lower St. Lawrence Estuary (Y. Simard, Institut Maurice-Lamontagne, personal communication). Due to this large range of uncertainty, we decided to use the mean annual biomass of 1,730,929 t or 16.674 t km^{-2} (SD = 23.481 t km^{-2}) estimated by Morissette et al. (2003) in the northern Gulf of St. Lawrence during the mid-1980s to calculate the P/B and Q/B ratios.

For sand lance, the resulting mean annual biomass estimate was 1,436 t or 0.014 t km^{-2} (SD = 0.009 t km^{-2}) for NAFO divisions 4RS. However, based on previous inverse modelling runs and due to the large uncertainty related to the biomass of this group, the previous value seemed to be too low to meet predator demands and was used as a lower limit. The upper limit was set to a tenth of the mean value (2.398 t km^{-2}) used by Morissette et al. (2003) in the northern Gulf of St. Lawrence during the mid-1980s. A mean biomass of 0.122 ± 0.167 t km^{-2} was used here.

For Arctic cod, the mean annual biomass estimate was 2,135 t or 0.021 t km^{-2} (SD = 0.027 t km^{-2}).

Production

There was no information available concerning the P/B ratios in the study area for these three groups. For capelin, production was assumed to be equal to biomass multiplied by natural mortality (M), plus the catch. Natural mortality was set to 0.6 yr^{-1} to reflect the biology of this short-lived species (F. Grégoire, Institut Maurice-Lamontagne, personal communication). When the mean, minimum, and maximum biomass values were used, we obtained a mean annual production of 10.038 ± 14.191 t km^{-2} yr^{-1} (range: 0.076–481.700 t km^{-2} yr^{-1}). The production value estimated by the inverse solution for capelin was 3.071 t km^{-2} yr^{-1} (P/B = 0.184 yr^{-1}).

Due to the lack of information, the P/B ratio for sand lance was also set to 0.6 yr^{-1}. When the minimum and maximum biomass values were used, we obtained a mean annual production of 0.073 ± 0.100 t km^{-2} yr^{-1} (range: 0.002–0.144 t km^{-2} yr^{-1}). The production value estimated by the inverse solution for sand lance was 0.124 t km^{-2} yr^{-1} (P/B = 1.017 yr^{-1}).

Due to the lack of information, the P/B ratio for Arctic cod was also set to 0.6 yr^{-1}. We used the minimum and maximum biomass values to obtain a production range of 0.001 to 0.031 t km^{-2} yr^{-1}, corresponding to a mean production of 0.011 ± 0.021 t km^{-2} yr^{-1}. The production value estimated by the inverse solution for Arctic cod was 0.014 t km^{-2} yr^{-1} (P/B = 0.667 yr^{-1}).

Consumption

Consumption rates for capelin, sand lance, and Arctic cod were taken from various sources. For all three species, the Q/B ratio was determined using FishBase (Froese and Pauly 2002). Q/B ratios for capelin and Arctic cod were estimated for a water temperature of 1°C, considering that these species are generally found near the cold intermediate layer in the Gulf of St. Lawrence. We obtained Q/B ratio values of 3.8 and 2.7 yr^{-1} for capelin and Arctic cod, respectively. For the two species of sand lance, the Q/B ratios estimated by FishBase at a temperature of 6°C for American sand lance and 1°C for northern sand lance were 5.0 and 8.5 yr^{-1}, respectively.

Other studies on the consumption of capelin were available. We used a second estimate based on the feeding ecology of capelin in the estuary and western Gulf of St. Lawrence (Vesin et al. 1981). The daily ration was estimated at 5.00% body mass in summer and 2.50% body mass in winter, giving a mean of 3.75% of body mass per day. From these values, the mean annual Q/B ratio was estimated to be 13.688 yr^{-1}. A third Q/B estimate was determined from a summer study on Barents Sea capelin (Ajiad and Pushaeva 1991). Daily ration was estimated to be between 1.47% and 2.00% of the body mass, resulting in an average Q/B ratio of 6.333 yr^{-1}. Finally, Panasenko (1981) estimated a Q/B ratio of 27.558 yr^{-1} in another study in the Barents Sea. When the mean, minimum, and maximum biomass values as well as the four previous Q/B ratios were used, we obtained a consumption range of 0.267 to 22,122.514 t km^{-2} yr^{-1}. Based on the previous mean production (10.038 t km^{-2} yr^{-1}) for capelin and the minimum and maximum GE limits (10–30%), we obtained consumption values of 33.461 and 100.384 t km^{-2} yr^{-1}. We decided to use 0.267–100.384 t km^{-2} yr^{-1} as lower and upper limit constraints, corresponding to a mean annual consumption of 50.326 ± 70.793 t km^{-2} yr^{-1}. The consumption value estimated by the inverse solution was 15.486 t km^{-2} yr^{-1} (Q/B = 0.929 yr^{-1}) for capelin.

For sand lance, one other study conducted on Georges Bank was available (Gilman 1994). Daily rations (% body mass) of adults throughout the year were averaged, resulting in a mean Q/B ratio of 8.160 yr^{-1}. When the minimum and maximum biomass values and the three previous Q/B ratios were used, we obtained a consumption range of 0.019 to 0.176 t km^{-2} yr^{-1}. Based on the mean production (0.073 t km^{-2} yr^{-1}) for sand lance and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.244 and 0.731 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.122 t km^{-2} yr^{-1} as the lower limit. The resulting lower and upper consumption limits were 0.122 and 0.731 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.426 ± 0.431 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.520 t km^{-2} yr^{-1} for sand lance, representing a Q/B ratio of 4.274 yr^{-1}.

Finally, in addition to the FishBase value, a second Q/B ratio (3.941 yr^{-1}) was available for Arctic cod from Canadian arctic waters (Hop et al. 1997). In this study, mean daily rations (% body mass per day) of juvenile and adult Arctic cod were estimated. When the minimum and maximum biomass values and the two previous Q/B ratios were used, we obtained a consumption range of 0.005 to 0.205 t km^{-2} yr^{-1}. Based on the mean production (0.011 t km^{-2} yr^{-1}) for Arctic cod and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.036 and 0.108 t km^{-2} yr^{-1}. However, assuming that this species would eat at least as much food as its biomass ($Q/B \geq 1$), we used 0.021 t km^{-2} yr^{-1} as the lower limit. The resulting lower and upper consumption limits were 0.021 and 0.205 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.113 ± 0.130 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.066 t km^{-2} yr^{-1} for Arctic cod, representing a Q/B ratio of 3.200 yr^{-1}.

Diet composition

For capelin, the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and by Jangaard (1974) for the North Atlantic were used. Main prey items were copepods (*Temora longicornis*, *Calanus finmarchicus*, and *Pseudocalanus minutus*) and euphausiid eggs. We used also the study of Vesin et al. (1981) in the estuary and western Gulf of St. Lawrence. In that study, euphausiids and copepods were the main prey (59 and 41%, respectively). The final diet compositions are shown in Table 13.

The diet composition of sand lance was taken from Scott (1973), who examined fish caught on the Scotian Shelf. From a total of 130 stomachs, copepods, polychaete larvae, and euphausiids were the main prey items (Table 13).

There was no diet data available for Arctic cod from the Gulf of St. Lawrence. Instead, a study on fish from the western Barents Sea (Lonne and Gulliksen 1989) and the diet composition estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf were used to determine the resulting diet composition. Copepods and amphipods were the most important prey items found in Arctic cod stomachs. The final diet compositions are shown in Table 13.

Table 13. Diet compositions of capelin, sand lance, and Arctic cod used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. For groups with the CV indicated (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Capelin					Sand lance (CV= 50%)				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin	1.4	2.0	**0.0**	**2.8**	1.6					
Sand lance	1.4	2.0	**0.0**	**2.8**	0.0					
Arctic cod										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp										
Large crustacea										
Echinoderms										
Molluscs										
Polychaetes										
Other bent. inver.	**0.0**	0.0	0.0	0.0	0.0	**0.0**		0.0	0.1	0.0
Large zooplankton	46.5	17.9	**34.5**	**59.9**	48.7	16.9		**8.4**	**25.3**	21.8
Small zooplankton	50.7	19.8	**37.5**	**65.5**	49.7	83.0		**41.5**	**100.0**	78.2
Phytoplankton						**0.1**		0.0	0.1	0.1
Detritus										
Total	100.0		72.0	131.0	100.0	100.0		50.0	125.4	100.0
TRN	5					4				

Table 13. Cont.

	Arctic cod				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin	1.9	2.7	**0.0**	**3.8**	1.2
Sand lance					
Arctic cod	**0.1**	0.1	0.0	0.2	0.1
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	34.4	41.8	**4.8**	**64.0**	27.2
Small zooplankton	63.6	44.7	**32.0**	**95.2**	71.5
Phytoplankton					
Detritus					
Total	100.0		36.8	163.2	100.0
TRN	4				

Pelagic feeders

Background

The pelagic feeders are also an important part of the ecosystem, and some species are commercially fished. Three boxes are designed to represent these species: large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders.

The large pelagic feeder group includes spiny dogfish (*Squalus acanthias*), pollock (*Pollachius virens*), and silver hake (*Merluccius bilinearis*). The most abundant large pelagic

feeder in NAFO divisions 4RS is spiny dogfish (79% of biomass). Juveniles of these species were classified as either piscivorous or planktivorous small pelagic feeders according to juvenile feeding behaviour.

The piscivorous small pelagic feeders group includes Atlantic mackerel (*Scomber scombrus*) and short-finned squid (*Illex illecebrosus*). Atlantic mackerel was the most important in terms of biomass (close to 100% of biomass) and was therefore considered the key species for the group. Mackerel populations in the northwest Atlantic form a complex stock that overwinters off the New England coast. A part of this complex stock then migrates northwards in May and June after spawning in the New Jersey Bight area and the southern Gulf of St. Lawrence (Moores et al. 1975). After spawning near the Îles-de-la-Madeleine, they disperse throughout the Gulf for the rest of the summer.

The planktivorous small pelagic feeders group includes Atlantic herring (*Clupea harengus*), Atlantic argentine (*Argentina silus*), planktivorous myctophids, and other mesopelagics. Atlantic herring, the only commercially fished species, was the most important in terms of biomass (99% of biomass) and was therefore considered the key species for the group. The spring-spawning population congregates off the west coast of Newfoundland and in and around St. George's Bay, while the autumn-spawning stock regroups further up the coast, north of Point Riche, to reproduce (McQuinn et al. 1999). Outside of the spawning season, these two stocks are mainly found in St. George's Bay in the spring, north of Point Riche and in the Strait of Belle Isle in the summer, and off Bonne Bay in the fall (McQuinn et al. 1999).

Catch

For the large pelagic feeders, landings for pollock (the only species for which data were available) were 4.17×10^{-5} t km^{-2} yr^{-1} (SD = 7.23×10^{-5} t km^{-2} yr^{-1}) (NAFO 1999). The inverse solution estimated a catch value of 4.53×10^{-5} t km^{-2} yr^{-1}.

Concerning piscivorous small pelagic feeders, the mean landings in NAFO divisions 4RS for 1994–96 were 3,060 t or 2.95×10^{-2} t km^{-2} yr^{-1} (SD = 8.80×10^{-3} t km^{-2} yr^{-1}) (Grégoire and Gilbert 1998). The inverse solution estimated a catch value of 2.95×10^{-2} t km^{-2} yr^{-1}.

Finally, for the planktivorous small pelagic feeders, the average landings in the study area during the 1994–96 period were 14,893 t or 1.43×10^{-1} t km^{-2} yr^{-1} (SD = 2.56×10^{-2} t km^{-2} yr^{-1}) (McQuinn et al. 1999). The inverse solution estimated a catch value of 1.46×10^{-1} t km^{-2} yr^{-1}.

Biomass

For the large pelagic feeders, biomass was calculated from scientific research survey data covering NAFO divisions 4RS during the 1994–1996 period. Biomass estimates were only available for silver hake, pollock, and spiny dogfish. The biomasses of all three species were then summed to obtain an estimate for the group. The mean biomass for the large pelagic feeders was estimated to be 3,382 t or 0.033 t km^{-2} (SD = 0.012 t km^{-2}).

Biomass estimates for Atlantic mackerel were derived from an egg production index calculated for 1983 to 1996 for the southern Gulf of St. Lawrence (F. Grégoire, unpublished data). We did not apply a residence time factor to reduce biomass by two (6 months outside the

Gulf) because this kind of fish feeds mainly during the summer period when they are in the Gulf. Only the 1994–1996 estimates were used to calculate the mean annual biomass. After spawning near the Îles-de-la-Madeleine, mackerel in the Gulf disperse throughout the entire area (NAFO divisions 4RS and 4T). There is a little information about the proportion of mackerel that moves into the northern (4RS) versus southern (4T) Gulf. We assumed that one third of the biomass moved into 4RS while the other two thirds were distributed in 4T. Knowing that the northern Gulf represents 59.7% of the trawlable surface area of the entire Gulf of St. Lawrence, mackerel biomass was estimated to be 57,978 t or 0.558 t km^{-2} (SD = 0.448 t km^{-2}).

For the planktivorous small pelagic feeders, the average biomass of herring (the key species for the group) during the 1994–96 period in the eastern part of the study area (NAFO division 4R) was taken from the sequential population analysis (SPA) by McQuinn et al. (1999). Since herring populations in 4S are considered to be small and data for this region were unavailable, it was assumed that the 4R population represented all the herring in the study area. The total biomass was 103,612 t or 1.617 t km^{-2}. The biomasses of Atlantic argentine and planktivorous myctophids in the study area, which were estimated from scientific research survey data, were 961 t (or 0.009 t km^{-2}) and 357 t (or 0.003 t km^{-2}), respectively, during the same period. Total biomass for the planktivorous small pelagic feeders group was 1.630 t km^{-2} (SD = 0.240 t km^{-2}).

Production

Since there was no information on specific P/B ratios for these species in the study area, it was assumed that production was equal to biomass multiplied by natural mortality (M), plus the catch. For the large pelagic feeders, natural mortality was assumed to be 0.15 yr^{-1} because one of the principal species, spiny dogfish, is a large, long-living fish with a relatively low natural mortality (Scott and Scott 1988). The production value was 0.005 t km^{-2} yr^{-1} (range: 0.003–0.007 t km^{-2} yr^{-1}) for the large pelagic feeders. However, the inverse solution estimated a production of 0.009 t km^{-2} yr^{-1}, representing a P/B of 0.262 yr^{-1}. The production estimate for the large pelagic feeders was higher than the initial upper limit used as a constraint in inverse modelling. This suggested that either biomass or natural mortality (M) was underestimated. If the biomass was properly estimated (0.033 t km^{-2}), then natural mortality should be equal to 0.26 yr^{-1} to obtain a production of 0.009 t km^{-2} yr^{-1}. But if the natural mortality (0.15 yr^{-1}) was correctly estimated, then the biomass should be equal to 0.057 t km^{-2} to obtain a production of 0.009 t km^{-2} yr^{-1}.

For the piscivorous small pelagic feeders, in the absence of better information, we assumed a value of 0.2 yr^{-1} for natural mortality, which was also the value used in the SPA for Atlantic herring, the key species of the planktivorous small pelagic feeders (McQuinn et al. 1999). The production value was 0.137 t km^{-2} yr^{-1} (range: 0.080–0.200 t km^{-2} yr^{-1}) for the piscivorous small pelagic feeders. The inverse solution estimated a production of 0.196 t km^{-2} yr^{-1}, representing a P/B of 0.351 yr^{-1}.

For the planktivorous small pelagic feeders, natural mortality was assumed to be 0.2 yr^{-1} (McQuinn et al. 1999). The production value was 0.454 t km^{-2} yr^{-1} (range: 0.403–0.499 t km^{-2} yr^{-1}). The inverse solution estimated a production of 0.495 t km^{-2} yr^{-1}, representing a P/B of 0.304 yr^{-1}.

Consumption

For the large pelagic feeders, FishBase made available two Q/B estimates (3.850 and 4.260 yr^{-1}) for silver hake from American waters, one Q/B estimate (4.760 yr^{-1}) for pollock from Canadian waters, and one Q/B estimate (4.770 yr^{-1}) for spiny dogfish also from Canadian waters (Froese and Pauly 2002). Three other consumption estimates were also available for silver hake. Edwards and Bowman (1979) studied the food consumed by continental shelf fish. A total of 17,000 stomachs obtained from 1963 to 1974 on the continental shelf between New Jersey and Halifax were analyzed. These authors estimated a Q/B ratio of 11.315 yr^{-1} for silver hake. A Q/B ratio of 7.869 yr^{-1} was estimated from stomach content analysis and the estimation of daily ration for silver hake (Durbin et al. 1983). Finally, in another study, Cohen and Grosslin (1981) examined food consumption of fish from Georges Bank. Q/B ratios of 7.605 and 9.516 yr^{-1}, respectively, were estimated for silver hake and pollock. When the minimum and maximum biomass values and the different previous Q/B ratios were used, we obtained a consumption range of 0.096 to 0.355 t km^{-2} yr^{-1}. Based on the mean production (0.005 t km^{-2} yr^{-1}) for the large pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.016 and 0.048 t km^{-2} yr^{-1}. However, assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), we used 0.033 t km^{-2} yr^{-1} as the lower limit. The resulting lower and upper consumption limits were 0.033 and 0.355 t km^{-2} yr^{-1}, corresponding to a mean consumption of 0.194 ± 0.228 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.042 t km^{-2} yr^{-1} for the large pelagic feeders, representing a Q/B ratio of 1.297 yr^{-1}.

For the piscivorous small pelagic feeders, a Q/B estimate of 4.400 yr^{-1} for Atlantic mackerel was taken from FishBase. Also, Mehl and Westgard (1983) estimated mackerel consumption in the North Sea to be 6% of body mass per day (n = 3,674). A Q/B ratio of 2.190 yr^{-1} was thus estimated from this information. When the minimum and maximum biomass values and the different previous Q/B ratios were used, we obtained a consumption range of 0.529 to 3.852 t km^{-2} yr^{-1}. Based on the mean production (0.137 t km^{-2} yr^{-1}) for the piscivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 0.457 and 1.372 t km^{-2} yr^{-1}. However, assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), we used 0.558 t km^{-2} yr^{-1} as the lower limit. The resulting lower and upper consumption limits were 0.558 and 3.852 t km^{-2} yr^{-1}, corresponding to a mean consumption of 2.205 ± 2.329 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 0.782 t km^{-2} yr^{-1} for the piscivorous small pelagic feeders, representing a Q/B ratio of 1.400 yr^{-1}.

For planktivorous small pelagics, Q/B estimates were derived from Pauly (1989), Rudstam et al. (1992), and Fetter and Davidjuka (1996). During summer, specific consumption rates of herring in the Baltic Sea were estimated to be from 10 to 20% of the body mass per day for young-of-the-year fish larger than 5 cm, 7 to 13% for 1+ fish, and 4 to 5% for older age groups (Rudstam et al. 1992). During autumn, these consumption rates declined to 2 to 4% for all age classes. This resulted in an estimated annual Q/B of 13.688 yr^{-1}. Values taken from Pauly (1989) were 4.590 yr^{-1} for fish from Georges Bank and 10.100 yr^{-1} for fish from the North Sea. Finally, Fetter and Davidjuka (1996) estimated daily food consumption for different periods of the year. Mean values fluctuated widely between 0.2 and 1.3% of body mass per day, corresponding to an annual Q/B of 2.798 yr^{-1}. When the minimum and maximum biomass values and the different previous Q/B ratios were used, we obtained a consumption range of 3.954 to 25.840 t km^{-2} yr^{-1}.

Based on the mean production (0.454 t km^{-2} yr^{-1}) for the planktivorous small pelagic feeders and the minimum and maximum GE limits (10–30%), we obtained consumption values of 1.512 and 4.535 t km^{-2} yr^{-1}. However, assuming that these species would eat at least as much food as their biomass ($Q/B \geq 1$), we used 1.630 t km^{-2} yr^{-1} as the lower limit. The resulting lower and upper consumption limits were 1.630 and 25.840 t km^{-2} yr^{-1}, corresponding to a mean consumption of 13.735 ± 17.119 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 2.293 t km^{-2} yr^{-1} for the planktivorous small pelagic feeders, representing a Q/B ratio of 1.407 yr^{-1}.

Diet composition

The diet of the large pelagic feeders was assumed to be that of their key species, silver hake. Four sources of information were used. After analyzing a total of 498 silver hake digestive tracts, Bowman and Bowman (1980) found that three free-swimming crustaceans (i.e., *Crangon septemspinosa*, *Dichelopandalus leptocerus*, and *Monoculodes intermedius*) made up the largest part of the diet, accounting for 48% by mass. A second study examined the diet of 7,649 silver and red hake in the northwest Atlantic (Vinogradov 1983). In this study, the main prey items for silver hake were piscivorous small pelagic feeders and euphausiids. Also, on the Scotian Shelf, silver hake mainly consumed piscivorous small pelagic feeders and euphausiids (*M. norvegica*) (N = 2,855) (Waldron 1992). Finally, in another study on the Scotian Shelf, Langton and Bowman (1980) found that the main prey items of silver hake were Gadidae fish and euphausiids. We also used the diet compositions estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf (1985–1987 period) and by Savenkoff et al. (2004) for the southern Gulf of St. Lawrence (mid-1990s) for this group. The final diet composition is shown in Table 14.

Diet composition for the piscivorous small pelagic feeders were derived from three sources of information on Atlantic mackerel, the key species for this group. On the Scotian Shelf, the main prey in 199 mackerel stomachs were hyperid amphipods, euphausiids, and fish larvae (mainly blennoids and gadoids) (Kulka and Stobo 1981). The other diet study examined 359 mackerel stomachs from the Gulf of St. Lawrence and the Scotian Shelf (Grégoire and Castonguay 1989). In this study, the main prey species (in % abundance) were found to be nematodes (which were probably stomach parasites), copepods, and unidentified larvae. Finally, Darbyson et al. (2003) found in the southern Gulf that the main prey in 265 mackerel stomachs were capelin, euphausiids, and copepods. The resulting diet composition is shown in Table 14.

For the diet of the planktivorous small pelagics group, we used the diet composition estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf and the stomach content data available from NAFO division 4T (M. Hanson, DFO, Gulf Fisheries Centre, Moncton, New Brunswick, unpublished data) (Table 14). We used also the study of Darbyson et al. (2003). The resulting diet composition is shown in Table 14.

Table 14. Diet compositions of large pelagic feeders, piscivorous small pelagic feeders, and planktivorous small pelagic feeders used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large pelagic feeders					Piscivorous small pelagic feeders				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod	3.3	9.2	**0.0**	**12.9**	0.5	**0.0**	0.0	0.0	0.0	0.0
Large Green. halibut										
Small Green. halibut										
American plaice	**0.0**	0.0	0.0	0.0	0.0					
Flounders	1.9	5.1	**0.0**	**7.2**	1.1					
Skates	1.3	3.7	**0.0**	**5.2**	1.4					
Redfish	0.3	0.9	**0.0**	**1.3**	0.6					
Large demersals										
Small demersals	3.9	10.8	**0.0**	**15.3**	1.8	**0.0**	0.0	0.0	0.0	0.0
Capelin	2.6	7.1	**0.0**	**10.0**	6.1	13.2	21.6	**0.0**	**30.6**	10.0
Sand lance	3.2	8.6	**0.0**	**12.2**	0.0	**0.0**	0.0	0.0	0.0	0.0
Arctic cod	3.3	9.2	**0.0**	**12.9**	1.4	**0.0**	0.0	0.0	0.0	0.0
Large pelagics										
Pisci. small pelagics	17.0	46.7	**0.0**	**66.0**	3.7					
Plank. small pelagics	22.3	61.0	**0.0**	**86.3**	16.3	**0.0**	0.0	0.0	0.0	0.0
Shrimp	17.9	48.9	**0.0**	**69.1**	12.4	**0.2**	0.3	0.0	0.4	0.2
Large crustacea	0.6	1.5	**0.0**	**2.1**	1.0					
Echinoderms	0.6	1.6	**0.0**	**2.3**	1.4					
Molluscs						**0.2**	0.3	0.0	0.4	0.2
Polychaetes	1.2	3.1	**0.0**	**4.5**	3.9					
Other ent. inver.	6.0	16.5	**0.0**	**23.3**	18.0					
Large zooplankton	14.1	38.6	**0.0**	**54.6**	29.3	47.0	64.1	**8.9**	**99.6**	47.5
Small zooplankton	0.5	1.3	**0.0**	**1.8**	1.2	39.4	64.4	**0.0**	**91.1**	42.2
Phytoplankton										
Detritus										
Total	100.0		0.0	387.1	100.0	100.0		8.9	222.0	100.0
TRN	18					10				

Table 14. Cont.

	Planktivorous small pelagic feeders				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin	1.8	2.9	**0.0**	**4.0**	0.7
Sand lance	**0.1**	0.2	0.0	0.3	0.1
Arctic cod					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp	6.2	9.7	**0.0**	**13.7**	0.0
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.	4.5	7.1	**0.0**	**10.0**	9.1
Large zooplankton	42.3	66.2	**0.0**	**93.7**	40.9
Small zooplankton	45.1	70.7	**0.0**	**100.0**	49.2
Phytoplankton					
Detritus					
Total	100.0		0.0	221.7	100.0
TRN	6				

Crustaceans

Background

Lobster is not included here because only waters deeper than 37 m were considered. The main crustaceans of the northern Gulf of St. Lawrence ecosystem are shrimp and snow crab. Both are exploited commercially.

The shrimp group consists of several species of penaeid and caridean shrimp and is represented by the key species northern shrimp, *Pandalus borealis*, which dominates the biomass

and is fished commercially. Generally, shrimp are found throughout the Estuary and the northern Gulf of St. Lawrence at depths of 150–350 m, but migrations do occur during breeding (the females migrate to shallower waters at the channel heads) and feeding (at night, they leave the ocean floor to feed on small planktonic organisms) (DFO 2000).

The snow crab (*Chionoecetes opilio*) represents the key species of the large crustacean group, which also includes other species such as toad crabs (*Hyas* spp.). Snow crab is highly exploited in the northern Gulf of St. Lawrence, particularly along Québec's North Shore.

Catch

Information on commercial landings of northern shrimp are available since 1982 for the three management units in the northern Gulf: Sept-Îles, Anticosti, and Esquiman (Savard 1999). The annual total landings from 1994 to 1996 were 13,075 t or 1.26×10^{-1} t km^{-2} yr^{-1} (SD = 4.81×10^{-2} t km^{-2} yr^{-1}). The inverse solution estimated a catch value of 1.18×10^{-1} t km^{-2} yr^{-1}.

For snow crab, a mean of 6,799 t was taken annually between 1994 and 1996, resulting in total landings of 6.55×10^{-2} t km^{-2} yr^{-1} (SD = 3.34×10^{-3} t km^{-2} yr^{-1}) (Dufour and Dallaire 1999). The inverse solution estimated a catch value of 6.55×10^{-2} t km^{-2} yr^{-1}.

Biomass

Shrimp biomass was calculated from scientific research survey data covering NAFO divisions 4RS during the 1994–1996 period. Mean biomass was 63,872 t or 0.615 t km^{-2} (SD = 0.230 t km^{-2}).

Current snow crab assessments do not estimate the total biomass in the Gulf of St. Lawrence. Biomass for this group was estimated using CPUE data for the period 1994–1996. Using the Leslie method (Leslie and Davis 1939), we can obtain the biomass of snow crab available to fishing gear. These data do not include females or immature males that are too small and avoid capture. However, from 1989 to 1998, a complete bottom trawl survey was conducted in baie Sainte-Marguerite (B. Sainte-Marie, Institut Maurice-Lamontagne, personal communication). Using these data, a ratio of commercial biomass to non-commercial biomass was computed. Assuming that size structure is the same throughout the Gulf, this ratio was used to transform the commercial biomass estimated from CPUEs to total biomass estimates. In this way, we obtained a mean biomass estimate of 89,500 t or 0.862 t km^{-2} (SD = 0.204 t km^{-2}) for the 1994–1996 period.

Production

Due to the lack of information, it was assumed that production was equal to biomass multiplied by natural mortality (M), plus the catch. For shrimp, natural mortality was assumed to be 0.64 yr^{-1} (Fréchette and Labonté 1981). We estimated a production range between 0.323 and 0.596 t km^{-2} yr^{-1}, corresponding to an annual production of 0.431 ± 0.126 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.573 t km^{-2} yr^{-1}, representing a P/B of 0.931 yr^{-1}.

For snow crab, an assumed natural mortality of 0.2 yr^{-1} was used to take into account the high natural mortality of juveniles as well as the lower natural mortality of adults (B. Sainte-Marie, personal communication). Using minimum and maximum biomasses, this resulted in a production range of 0.217 to 0.237 t km^{-2} yr^{-1}, corresponding to an annual production of 0.227 ± 0.003 t km^{-2} yr^{-1}. The inverse solution estimated a production of 0.233 t km^{-2} yr^{-1}, representing a P/B of 0.271 yr^{-1}.

Consumption

In the absence of information on food consumption by northern shrimp, consumption was only estimated by using the gross growth efficiency (GE, the ratio of production to consumption). Based on the mean production (0.431 t km^{-2} yr^{-1}) for shrimp and the minimum and maximum GE limits (10–30%), we obtained two consumption values of 1.435 and 4.306 t km^{-2} yr^{-1}, corresponding to a mean consumption of 2.871 ± 2.030 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 2.741 t km^{-2} yr^{-1} for shrimp, representing a Q/B ratio of 4.455 yr^{-1}.

Snow crab consumption data were obtained from a study conducted in the Baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984). A daily ration of 0.4% of body mass was estimated, resulting in a Q/B ratio of 1.460 yr^{-1}. A second estimate was derived from a study of the physiological energetics of the snow crab (Thompson and Hawryluk 1990). The estimated Q/B ratio was 1.302 yr^{-1}. When the minimum and maximum biomass values and the two previous Q/B ratios were used, we obtained a consumption range of 1.122 to 1.259 t km^{-2} yr^{-1}. Based on the mean production (0.227 t km^{-2} yr^{-1}) for large crustaceans and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 0.757 and 2.272 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 0.757 and 2.272 t km^{-2} yr^{-1}, corresponding to a mean consumption of 1.515 ± 1.071 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 1.357 t km^{-2} yr^{-1} for large crustaceans, representing a Q/B ratio of 1.574 yr^{-1}.

Diet composition

For shrimp, feeding occurs in both the benthic and pelagic environments as a result of their daily vertical migrations. In their model, Bundy et al. (2000) assumed that 30% of the total diet was benthic and 70% was pelagic. Annelids, small crustaceans, detritus, and bottom plants were the main prey during the day while copepods and euphausiids were the principal prey items during the nocturnal migration. We used this diet composition (Table 15).

For snow crab, diet data were available from the baie des Chaleurs and the southern Gulf of St. Lawrence (Brêthes et al. 1984) as well as the west coast of Newfoundland (Wieczorek and

Hooper 1995). From the study by Brêthes et al. (1984), abundance estimates were multiplied by the mean mass of each prey to obtain biomass indices for the diet. The main prey items of the 480 snow crabs were polychaetes, gastropods, echinoderms, and decapods. In the study of Wieczorek and Hooper (1995) (n = 198 stomachs), the main components of the diet in terms of mass were annelids, echinoderms, and molluscs such as bivalves. We also used the diet composition estimated by Bundy et al. (2000) for the Newfoundland–Labrador Shelf, where the main prey were annelids, echinoderms, and molluscs. Finally, the diet composition estimated by Savenkoff et al. (2004) for the southern Gulf of St. Lawrence (mid-1990s) was also used to construct the upper and lower limits for this group. In that study, molluscs, echinoderms, and annelids were the main prey and there was also a high proportion of detrital matter (31%). The final diet composition for this group is shown in Table 15.

Table 15. Diet compositions of shrimp and large crustacea used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. For groups with the CV indicated (available only as point estimates): Min = mean – (mean x 50%), Max = mean + (mean x 50%). Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Shrimp (CV= 50%)					Large crustacea				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals						1.7	3.5	**0.0**	**5.0**	0.0
Capelin										
Sand lance										
Arctic cod										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp	**0.0**		0.0	0.0	0.0	1.7	3.3	**0.2**	**4.9**	0.4
Large crustacea						3.7	7.8	**0.0**	**11.1**	0.1
Echinoderms						10.9	22.3	**0.5**	**32.1**	7.3
Molluscs						25.0	46.1	**4.8**	**69.9**	22.6
Polychaetes	1.5		**0.8**	**2.3**	2.0	14.8	23.6	**5.5**	**38.8**	28.3
Other bent. inver.	1.5		**0.8**	**2.3**	1.8	16.7	35.0	**0.1**	**49.6**	18.8
Large zooplankton	12.0		**6.0**	**18.0**	15.6	13.3	27.6	**0.4**	**39.4**	11.4
Small zooplankton	24.0		**12.0**	**36.0**	26.1	1.6	3.5	**0.0**	**4.9**	1.0
Phytoplankton	8.5		**4.3**	**12.8**	11.7	**0.0**	0.0	0.0	0.0	0.0
Detritus	52.5		**26.3**	**78.8**	42.7	10.4	22.0	**0.0**	**31.1**	10.2
Total	100.0		50.0	150.0	100.0	100.0		11.5	286.9	100.0
TRN	7					11				

Benthic invertebrates

Background

The benthic invertebrates other than shrimp and crabs were divided into four groups: echinoderms, molluscs, polychaetes, and other benthic invertebrates. This last group consisted mainly of miscellaneous crustaceans, nematodes, and other meiofauna. Benthic data for the northern Gulf of St. Lawrence were lacking. Consequently, in many cases it was assumed that benthic biomass was similar to that of the Newfoundland–Labrador Shelf ecosystem (Bundy et al. 2000). The most recent comprehensive source of information on the benthos is a study carried out in 1980 under the auspices of the Mobil Oil Company on the Grand Banks of Newfoundland (Hutcheson et al. 1981).

Only part of the mollusc biomass, the soft body tissue, is transferred through the food web. This is confirmed by observations of huge shells beds on the ocean floor (Hutcheson et al. 1981). In order to reduce the biomass and account for soft body tissue only, the ratio of the body mass to whole mass of the mollusc *Mesodesma deauratum* was estimated. The mean ratio between blotted wet mass of tissue to whole mass for animals with a shell length between 30 and 35 mm was 0.166 ± 0.023 (n = 10; K. Gilkinson, DFO, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, unpublished data).

Catch

Polychaetes, echinoderms, and other benthic invertebrates were not exploited commercially in the study area during the 1994–1996 period. Only molluscs were commercially harvested. Commercial species are sea scallops (*Placopecten magellanicus*), soft-shelled clams (*Mya arenaria*), whelks (*Busycon* sp.), and periwinkles (*Littorina* sp.). Average annual landings were taken from the NAFO statistics and are 2,939 t or 2.83×10^{-2} t km^{-2} yr^{-1} (SD = 6.19×10^{-3} t km^{-2} yr^{-1}) (NAFO 1999). The inverse solution estimated a catch value of 2.87×10^{-2} t km^{-2} yr^{-1}. However, these different values were for the whole mass including the shell. The uncorrected catch estimate represented only 0.1% of total production estimate of molluscs (or total mortality). Consequently, a decrease in this value after correcting for soft body tissue should not have a large impact on the modelling results.

Biomass

The mean biomasses for 4RS were assumed to be the same as for 2J3KLNO and were 112.300 t km^{-2} for echinoderms, 42.100 t km^{-2} for molluscs, 10.500 t km^{-2} for polychaetes, and 7.800 t km^{-2} for other benthic invertebrates.

Production

There is no information available on production estimates of benthic invertebrates in the northern Gulf. All the estimates are taken from the literature for other areas.

Echinoderms

Warwick et al. (1978) estimated an annual production of 0.229 t km^{-2} yr^{-1} for echinoderms in Carmarthen Bay (South Wales, U.K.) while Buchanan and Warwick (1974) obtained an estimate of 0.108 t km^{-2} yr^{-1}. However, higher echinoderm productions have been reported in the New York Bight (70.108 t km^{-2} yr^{-1}; Steimle 1985) and on Georges Bank (64.221 t km^{-2} yr^{-1}; Steimle 1987). Production could thus range between 0.108 and 70.108 t km^{-2} yr^{-1}, corresponding to an annual production of 33.667 ± 38.755 t km^{-2} yr^{-1}. The inverse solution estimated a production of 32.920 t km^{-2} yr^{-1}, representing a P/B of 0.293 yr^{-1}.

Molluscs

For molluscs, Warwick et al. (1978) estimated an annual production of 3.824 t km^{-2} yr^{-1} in Carmarthen Bay (South Wales, U.K.) while Sanders (1956) estimated 4.671 t km^{-2} yr^{-1} in Long Island Sound. Higher production estimates were reported by Steimle (1985) (82.121 t km^{-2} yr^{-1}) and by Borkowski (1974) (23.530 t km^{-2} yr^{-1}), as well as lower estimates such as 0.600 t km^{-2} yr^{-1} in Buchanan and Warwick (1974). Production could thus range between 0.600 and 82.121 t km^{-2} yr^{-1}, corresponding to an annual production of 22.949 ± 34.282 t km^{-2} yr^{-1}. The inverse solution estimated a production of 69.072 t km^{-2} yr^{-1}, representing a P/B of 1.641 yr^{-1}.

Polychaetes

Estimates of the annual production of polychaetes ranged between 0.206 and 74.564 t km^{-2} yr^{-1} (0.206 t km^{-2} yr^{-1} in Buchanan and Warwick [1974], 0.939 t km^{-2} yr^{-1} in Warwick et al. [1978], 5.522 t km^{-2} yr^{-1} in Sanders [1956], 6.310 t km^{-2} yr^{-1} in Collie [1987], 8.250 t km^{-2} yr^{-1} in Peer [1970], 16.050 t km^{-2} yr^{-1} in Nichols [1975], 21.600 t km^{-2} yr^{-1} in Curtis [1977], and 74.564 t km^{-2} yr^{-1} in Steimle [1985]). This represented an annual production of 16.680 ± 24.487 t km^{-2} yr^{-1}. The inverse solution estimated a production of 23.889 t km^{-2} yr^{-1}, representing a P/B of 2.275 yr^{-1}.

Other benthic invertebrates

Estimates of annual production for other benthic invertebrates ranged between 0.517 and 15.677 t km^{-2} yr^{-1} (0.517 t km^{-2} yr^{-1} in Sheader [1977], 5.000 t km^{-2} yr^{-1} in Klein et al. [1975], 15.500 t km^{-2} yr^{-1} in Cederwall [1977], and 15.677 t km^{-2} yr^{-1} in Collie [1985]). This represented an annual production of 9.173 ± 7.631 t km^{-2} yr^{-1}. The inverse solution estimated a production of 7.738 t km^{-2} yr^{-1}, representing a P/B of 0.992 yr^{-1}.

Consumption

In the absence of information on food consumption, consumption values were estimated by taking gross growth efficiency (GE) between 0.09 and 0.30 (Christensen and Pauly 1992). For echinoderms, this produced a consumption range between 112.222 and 374.072 t km^{-2} yr^{-1}, corresponding to a mean consumption of 243.147 ± 185.156 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 119.850 t km^{-2} yr^{-1}, representing a Q/B ratio of 1.067 yr^{-1}.

For molluscs, this produced a consumption range between 76.497 and 254.991 t km^{-2} yr^{-1}, corresponding to a mean consumption of 165.744 ± 126.214 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 237.726 t km^{-2} yr^{-1}, representing a Q/B ratio of 5.647 yr^{-1}.

For polychaetes, this produced a consumption range between 55.601 and 185.336 t km^{-2} yr^{-1}, corresponding to a mean consumption of 120.468 ± 91.737 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 97.342 t km^{-2} yr^{-1}, representing a Q/B ratio of 9.271 yr^{-1}.

For other benthic invertebrates, this produced a consumption range between 30.578 and 101.926 t km^{-2} yr^{-1}, corresponding to a mean consumption of 66.252 ± 50.451 t km^{-2} yr^{-1}. The inverse solution estimated a consumption of 46.723 t km^{-2} yr^{-1}, representing a Q/B ratio of 5.990 yr^{-1}.

Diet composition

For echinoderms, diet information was taken from the three most abundant species in NAFO divisions 2J3KL: the sand dollar (*Echinarchnius parma*), the sea urchin (*Strongylocentrotus pallidus*), and the brittle star (*Ophiura robusta*). The resulting diet is 100% detritus (Bundy et al. 2000).

For molluscs, Bundy et al. (2000) analyzed the diet composition of a suspension feeder (*Macoma deauratum*), a deposit feeder (*Macoma calcarea*), and a suspension or detrital feeder (*Liocyma fluctuosa*). Suspension feeders feed on organic detrital matter that is resuspended in the water immediately above the sediment surface. Deposit feeders can be considered as detrital feeders. Thus, the molluscs are assumed to be detrital feeders of various forms and the diet of the mollusc group is 100% detritus. However, in shallower waters, molluscs could consume phytoplankton (M. Fréchette, Institut Maurice-Lamontagne, personal communication). This potential food was also accounted for in the final diet composition (Table 16).

The polychaetes are considered to have a diet of 100% detritus (Nesis 1965; Fauchald and Jumars 1979). However, recent studies at two deeper Laurentian trough stations (275 and 325 m depth) showed that polychaetes could also consume phytoplankton and that cannibalism could have a significant impact in the diet composition (Desrosiers et al. 2000). The resulting diet is shown in Table 16.

The key organisms for the other benthic invertebrate group are gammarid amphipods. These species feed mainly on organic detritus (Nesis 1965; Hutcheson et al. 1981).

Table 16. Diet compositions of molluscs and polychaetes used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Molluscs					Polychaetes				
Prey	Mean	± SD	Min	Max	Est	Mean	± SD	Min	Max	Est
Large cod										
Small cod										
Large Green. halibut										
Small Green. halibut										
American plaice										
Flounders										
Skates										
Redfish										
Large demersals										
Small demersals										
Capelin										
Sand lance										
Arctic cod										
Large pelagics										
Pisci. small pelagics										
Plank. small pelagics										
Shrimp										
Large crustacea										
Echinoderms										
Molluscs										
Polychaetes						13.4	16.5	**1.8**	**25.1**	9.1
Other bent. inver.										
Large zooplankton										
Small zooplankton										
Phytoplankton	5.0	7.1	**0.0**	**10.0**	10.0	43.3	8.2	**37.5**	**49.1**	48.5
Detritus	95.0	7.1	**90.0**	**100.0**	90.0	43.3	8.2	**37.5**	**49.1**	42.4
Total	100.0		90.0	110.0	100.0	100.0		76.7	123.3	100.0
TRN	2					3				

Large zooplankton

Background

Organisms and species representing this group are greater than 5 mm in length and include euphausiids, chaetognaths, hyperiid amphipods, jellyfish (cnidarians and ctenophores), mysids, tunicates, and ichthyoplankton. This group contains herbivorous (some euphausiid species), omnivorous (most euphausiids, hyperid amphipods, mysiids, and large tunicates), and carnivorous (chaetognaths and jellyfish) species.

Catch

There was no commercial fishery for species in this group during the 1994–96 period in the northern Gulf.

Biomass

Biomass was calculated from euphausiid data gathered in 1973 off Anticosti Island and in the northwestern Gulf of St. Lawrence (Sameoto and Jarosynski 1973). In the absence of more current information, it was assumed that euphausiid biomass was similar during the 1994–96 period. We used this value as a guesstimate for large zooplankton group. This gives a biomass estimate of 9.643 t km^{-2} (SD = 14.482 t km^{-2}) or 1,001,007 t for the study area.

Production

The euphausiid production estimate was obtained from several different sources. These sources included P/B ratios of 4.000 yr^{-1} for the Gulf of St. Lawrence (Berkes 1977), 2.750 yr^{-1} (range: 1.300–4.200 yr^{-1}; Lindley 1980) to 3.840 yr^{-1} (range: 1.300–6.300 yr^{-1}; Lindley 1982) for the North Sea, and 1.600 yr^{-1} for the northeast Atlantic off the west coast of Ireland (Mauchline 1985). Production could thus range between 14.000 and 35.000 t km^{-2} yr^{-1}, corresponding to an annual production of 26.578 ± 9.661 t km^{-2} yr^{-1}. The inverse solution estimated a production of 23.602 t km^{-2} yr^{-1}, representing a P/B of 2.448 yr^{-1}.

Consumption

Consumption was estimated from data on euphausiids in the Gulf of St. Lawrence (Sameoto 1976). This produced a consumption range between 46.370 and 207.938 t km^{-2} yr^{-1}. Based on the mean production (26.578 t km^{-2} yr^{-1}) for large zooplankton and the minimum and maximum GE limits (10–30%), we obtained two other consumption values of 88.594 and 265.781 t km^{-2} yr^{-1}. The resulting lower and upper consumption limits were 46.370 and 265.781 t km^{-2} yr^{-1}, corresponding to a mean consumption of 156.076 ± 155.147 t km^{-2} yr^{-1}. The inverse solution

estimated a consumption of 118.426 t km^{-2} yr^{-1} for large zooplankton, representing a Q/B ratio of 12.282 yr^{-1}.

Diet composition

No diet information was available for these species in the northern Gulf of St. Lawrence. In other areas, euphausiids feed on detritus, phytoplankton, chaetognaths, amphipods, and copepods (Mauchline 1980). Chaetognaths and jellyfish eat copepods (Sullivan 1980; Smayda 1993). The relative proportions of these prey in the resulting large zooplankton diet were 5% large zooplankton, 43% small zooplankton, 37% phytoplankton, and 15% detritus (Bundy et al. 2000) (Table 17).

Table 17. Diet composition of large zooplankton used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Large zooplankton (> 5 mm)				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Sand lance					
Arctic cod					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton	5.0	5.7	**0.0**	**10.7**	3.7
Small zooplankton	43.0	7.1	**38.0**	**48.0**	38.0
Phytoplankton	37.0	30.7	**6.3**	**67.7**	48.3
Detritus	15.0	7.1	**10.0**	**20.0**	10.0
Total	100.0		54.3	146.4	100.0
TRN	4				

Small zooplankton

Background

The small zooplankton includes zooplankton less than or equal to 5 mm in length. Copepods, mainly *Calanus finmarchicus* and *Oithona similis*, are the most numerous small zooplankton. Also included in the small zooplankton category are meroplankton and tunicates < 5 mm, which are generally underestimated by sampling gear (Strong 1981). The most recent comprehensive source of information on the small zooplankton in the northern Gulf of St. Lawrence was a study carried out from July 1992 to June 1994 during the Canadian Joint Global Ocean Flux Study (JGOFS) program (Roy et al. 2000). Calanoid copepods accounted for 20 to 70% of the numerical abundance of all zooplankton species present, with *Calanus finmarchicus/glacialis* (not distinguished in the counts) and *C. hyperboreus* generally dominant among the mid-sized organisms (i.e., those retained by the 500 µm mesh). The greatest numbers of the *Calanus* spp. were observed at the deeper Laurentian trough stations. The small cyclopoid copepod *Oithona similis* was also very abundant, ranging from 20 to 70% of the numerical abundance of all species.

Catch

None.

Biomass

Zooplankton was sampled around mid-day and mid-night, using a WP-2 net (mesh size = 200 µm) (Roy et al. 2000). Zooplankton was sampled around mid-day and mid-night, using a WP-2 net (mesh size = 200 µm) (Roy et al. 2000). Data from these day and night hauls were averaged over the top 150 m at three stations (Anticosti Gyre, Anticosti Channel, and Cabot Strait stations) for each season (Savenkoff et al. 2000). The mean biomass for the entire area was 3,534 ± 1,814 mg C m^{-2} for all the small zooplankton. The range was wide and we assumed that it should account for the heterotrophic protozoan (flagellates, dinoflagellates, and ciliates) biomass (1,177 ± 580 mg C m^{-2}). Using a conversion factor of 10 g wet mass = 1g C (Christensen and Pauly 1992), we obtained 35.336 ± 18.137 t wet mass km^{-2}. The minimum–maximum range was of 17.199 to 53.473 t wet mass km^{-2}. Based on de Lafontaine et al. (1991; see their Fig. 7), another minimum–maximum biomass range was estimated as 1–24 g dry mass m^{-2} or 5.000–120.000 t wet mass km^{-2} yr^{-1} for small zooplankton. The resulting biomass could thus range between 5.000 and 120.000 t km^{-2}, corresponding to a mean value of 50.000 ± 81.317 t km^{-2}.

Production

Production (94.76 mg C m^{-2} d^{-1} or 345.886 t wet mass km^{-2} yr^{-1}) was estimated from Vézina et al. (2000). However, de Lafontaine et al. (1991) estimated 1 g C m^{-2} mo^{-1} (or 120.00 t wet mass

km^{-2} yr^{-1}) for secondary production of copepod-sized organisms. Production could thus range between 120.000 and 345.886 t km^{-2} yr^{-1}, corresponding to an annual production of 232.943 ± 159.725 t km^{-2} yr^{-1}. The inverse solution estimated a production of 282.899 t km^{-2} yr^{-1}, representing a P/B of 5.658 yr^{-1}.

Consumption

Vézina et al. (2000) estimated a minimum consumption value (120.04 mg C m^{-2} d^{-1} or 438.135 t wet mass km^{-2} yr^{-1}) for the summer and fall periods and a maximum (425.94 mg C m^{-2} d^{-1} or 1,554.666 t wet mass km^{-2} yr^{-1}) value for the winter and spring periods. These lower and upper limits, along with the corresponding mean (272.99 ± 216.30 mg C m^{-2} d^{-1} or 996.401 ± 789.507 t wet mass km^{-2} yr^{-1}) were used. The inverse solution estimated a consumption of 921.864 t km^{-2} yr^{-1}, representing a Q/B of 18.437 yr^{-1}.

Diet composition

The small zooplankton feed on both autotrophic and heterotrophic microplankton. However, heterotrophic microplankton (heterotrophic dinoflagellates, ciliates, and small metazoans) were included in the small zooplankton group here. Moreover, there is ample empirical evidence that mesozooplankton is omnivorous (Stoecker and Capuzzo 1990; Ohman and Runge 1994; Vézina et al. 2000). Small zooplankton, phytoplankton, and detritus were thus assumed to be potentially accessible to small zooplankton (Table 18).

Table 18. Diet composition of small zooplankton used in modelling. Est: diet estimates by the inverse model; TRN: number of trophic relations; SD: standard deviation. All values are percentages except TRN. Empty cells indicate that a prey item was never found whereas "0.0" indicates that it was found in very small amounts. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Small zooplankton (< 5 mm)				
Prey	Mean	± SD	Min	Max	Est
Large cod					
Small cod					
Large Green. halibut					
Small Green. halibut					
American plaice					
Flounders					
Skates					
Redfish					
Large demersals					
Small demersals					
Capelin					
Sand lance					
Arctic cod					
Large pelagics					
Pisci. small pelagics					
Plank. small pelagics					
Shrimp					
Large crustacea					
Echinoderms					
Molluscs					
Polychaetes					
Other bent. inver.					
Large zooplankton					
Small zooplankton	12.5	12.5	**9.3**	**26.9**	11.4
Phytoplankton	54.1	47.6	**0.0**	**67.3**	64.9
Detritus	33.4	35.2	**23.4**	**73.1**	23.7
Total	100.0		32.7	167.3	100.0
TRN	3				

Phytoplankton

Background

Most information on phytoplankton in the northern Gulf of St. Lawrence was derived from a study carried out from July 1992 to June 1994 during the Canadian Joint Global Ocean Flux Study (JGOFS) program (Savenkoff et al. 2000). These authors described the seasonal changes in photosynthetic production, respiration, sinking flux of organic carbon, and food web structure in the Gulf of St. Lawrence over a two-year period.

Diatoms were the most abundant phytoplankton in terms of both cell numbers and biovolumes during spring and winter. A mixture of autotrophic and mixotrophic organisms including Cryptophytes, diatoms, dinoflagellates, Prasinophytes, and mixotrophic *Stombidium* spp. (in the Spirotrichea) dominated during summer and fall. Prymnesiophytes were important in terms of cell numbers during spring and winter. The diatoms were dominated by *Chaetoceros affinis*, *Chaetoceros* spp., *Leptocylindrus minimus*, and *Thalassiiosira nordenskioldii* during winter and by *Thalassiiosira* spp. (*T. punctigera*, *T. nordenskioldii*, *T. pacifica*, and *T. bioculata*) and *Fragilariopsis* spp. (*F. oceanica* and *F. cylindrus*) during spring. During summer, the importance of diatoms in the phytoplankton composition was lower, with the majority observed being smaller centric diatoms such as *Minidiscus* sp., *Chaetoceros minimus*, and occasionally larger *Coscinodiscus* spp.

Phytoplankton biomass and production are the only two parameters required for modelling. There is no harvest, and since they are autotrophs, there is no consumption and no diet.

Biomass

Phytoplankton biomass is measured as chlorophyll *a* biomass. Mean annual chlorophyll *a* biomass (47 ± 33 mg CHL m^{-2}) was estimated as the mean of the seasonal biomass averages integrated over the euphotic zone (defined as the depth of 1% surface incident radiation) (Savenkoff et al. 2000). To facilitate comparisons with other studies in the Gulf of St. Lawrence, phytoplankton carbon biomass was estimated by converting measured chlorophyll *a* concentrations (CHL) to carbon (C) using a C/CHL ratio of 50 (Rivkin et al. 1996; Savenkoff et al. 2000).

The mean biomass for the entire area was 2.3 ± 1.6 g C m^{-2} or 23.411 ± 16.474 t km^{-2}, using a conversion factor of 10 g wet mass = 1g C (Christensen and Pauly 1992). The minimum–maximum range was of 5.009 to 45.452 t km^{-2}.

Primary Production

Primary production was estimated from the same data sources as described above. After correcting for phytoplankton respiration (75 ± 38 mg C m^{-2} d^{-1}), a value of 599 ± 303 mg C m^{-2} d^{-1} was estimated over the euphotic zone (Savenkoff et al. 2000). This represented 218.55 ± 110.75 g C m^{-2} yr^{-1} or 2,185.476 ± 1,107.451 t km^{-2} yr^{-1}. The minimum–maximum range was of

1,078,025 to 3,292,927 t wet mass km^{-2} yr^{-1}. The inverse solution estimated a production of 1,129,019 t km^{-2} yr^{-1}, representing a P/B of 48.226 yr^{-1}.

Detritus

Biomass

The detritus mass was estimated using an empirical relationship derived by Pauly et al. (1993) that relates detritus biomass to primary productivity and euphotic depth.

$$\log_{10} D = -2.41 + 0.954 \log_{10} PP + 0.863 \log_{10} E \quad (8)$$

where D is the standing stock of detritus (g C m^{-2}), PP is primary productivity (g C m^{-2} yr^{-1}), and E is the euphotic depth (m).

The annual value for primary production was 245.9 ± 109.9 g C m^{-2} yr^{-1}. The euphotic depth is estimated from Savenkoff et al. (2000) as 28.2 ± 5.9 m. The primary production estimate and euphotic depth were substituted into equation 8, giving a range of detritus biomass estimates from 6.2 to 22.2 g C m^{-2}, or 61,630 to 222,058 t km^{-2}, using a conversion factor of 10 g wet mass = 1g C (Christensen and Pauly 1992). This resulted in a mean detritus biomass of 132,608 ± 113,440 t km^{-2}.

Here, bacteria were considered part of the detritus compartment. Detritus estimates had a wide range, and it was assumed that this range should allow for the bacterial biomass (bacterial biomass: 184 ± 40 mg C m^{-2} or 1.8 ± 0.4 t km^{-2}; Savenkoff et al. 2000).

Respiration

Detritus is usually assumed not to respire. However, as bacteria were considered part of the detritus in this study, there would be respiration involved. Based on Savenkoff et al. (2000), we estimated a planktonic respiration (organisms < 200 µm including bacteria) close to 162 ± 33 mg C m^{-2} d^{-1} and 383 ± 152 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively, in the euphotic zone of the northern Gulf of St. Lawrence. Vézina et al. (2000) applied inverse modelling to the data collected from July 1992 to June 1994 to estimate trophic flows in the planktonic food web and to calculate export fluxes consistent with mass balance. These authors estimated that phytoplankton respiration represented 8 and 20% of the primary production for the winter–spring and summer–fall periods, respectively (R_{PHY} = 80 ± 41 mg C m^{-2} d^{-1} for winter–spring and 70 ± 64 mg C m^{-2} d^{-1} for summer–fall). By subtracting, we could estimate a detrital (or bacterial) respiration of 82 ± 53 mg C m^{-2} d^{-1} and 313 ± 165 mg C m^{-2} d^{-1} for the winter–spring and summer–fall periods, respectively. This represented 198 ± 86 mg C m^{-2} d^{-1} or 72 ± 32 g C m^{-2} yr^{-1} for the euphotic zone.

Based on the data collected from July 1992 to June 1994 at three stations located in the Laurentian Channel, Savenkoff et al. (1996) estimated a bacterial respiration of 44 ± 9 mg C m^{-2} d^{-1} or 16 ± 28 g C m^{-2} yr^{-1} in the aphotic layer (up to 300 m depth). By adding bacterial respiration values estimated in the euphotic and aphotic layers, a total detrital respiration could be estimated

as 88.3 ± 42.4 g C m^{-2} yr^{-1} or 882.961 ± 423.748 t km^{-2} yr^{-1} (range: 459.213–1,306.710 t km^{-2} yr^{-1}). The inverse solution estimated a detrital respiration of 507.290 t km^{-2} yr^{-1}.

Export

The fraction of the organic carbon that is not returned to the water column but is buried and preserved within the sediment represents the export of detritus. Silverberg et al. (2000) estimated a burial flux of particulate organic carbon between 0.46 and 0.53 mol C m^{-2} yr^{-1} at the Anticosti Gyre and Cabot Strait stations, respectively. This represented a detrital export close to 5.9 ± 0.6 g C m^{-2} yr^{-1} or 5.94 x 10^{1} ± 0.59 x 10^{1} t km^{-2} yr^{-1}. The inverse solution estimated a detrital export of 5.35 x 10^{1} t km^{-2} yr^{-1}.

Data synthesis

Data about biomass, export (here equal to commercial catch), production, and consumption are summarized in Tables 19 and 20.

Table 19. Observed biomass and export for each group used as input parameters for modelling for the 1994–1996 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Cetaceans	0.233	0.014	0.219	0.247	**3.75×10^{-4}**	2.09×10^{-5}	3.60×10^{-4}	3.90×10^{-4}	3.70×10^{-4}
Harp seals	0.127	0.005	0.123	0.132	1.54×10^{-2}	1.44×10^{-2}	**6.31×10^{-3}**	**3.21×10^{-2}**	7.94×10^{-3}
Hooded seals	0.005	0.000	0.005	0.005	**2.02×10^{-5}**	1.98×10^{-5}	9.63×10^{-7}	4.05×10^{-5}	2.27×10^{-5}
Grey seals	0.035	0.002	0.033	0.036	**1.22×10^{-5}**	2.12×10^{-5}	0	3.67×10^{-5}	1.29×10^{-5}
Harbour seals	0.004	0.000	0.004	0.004					
Seabirds	0.004	0.002[b]			3.35×10^{-4}	2.55×10^{-4}[c]	**8.00×10^{-5}**	**5.89×10^{-4}**	2.28×10^{-4}
Large cod	0.268	0.008	0.259	0.273	**3.26×10^{-3}**	1.22×10^{-3}	1.43×10^{-3}	3.26×10^{-3}	2.87×10^{-3}
Small cod	0.038	0.022	0.015	0.059					
Large Green. halibut	0.231	0.108	0.130	0.345	**9.49×10^{-3}**	3.88×10^{-3}	7.18×10^{-3}	1.26×10^{-2}	9.51×10^{-3}
Small Green. halibut	0.204	0.095	0.138	0.314					
Amer. plaice	0.964	0.216	0.715	1.098	**1.78×10^{-3}**	6.46×10^{-4}	1.04×10^{-3}	2.25×10^{-3}	1.88×10^{-3}
Flounders	0.064	0.029	0.036	0.094	**1.62×10^{-3}**	3.45×10^{-4}	1.42×10^{-3}	2.01×10^{-3}	1.63×10^{-3}
Skates	0.161	0.016	0.150	0.179	**1.11×10^{-3}**	2.96×10^{-4}	8.38×10^{-4}	1.43×10^{-3}	1.09×10^{-3}
Redfish	1.432	0.623	1.051	2.151	**1.67×10^{-2}**	4.00×10^{-2}	2.89×10^{-4}	4.94×10^{-2}	2.16×10^{-2}
Large demersals	0.176	0.030	0.141	0.195	**1.78×10^{-3}**	1.12×10^{-3}	5.88×10^{-4}	2.80×10^{-3}	1.79×10^{-3}
Small demersals	0.241	0.292	0.034	0.448					
Capelin	16.674	23.481	0.070	802.777	**2.45×10^{-2}**	4.97×10^{-2}	1.01×10^{-3}	6.49×10^{-2}	3.42×10^{-2}
Sand lance	0.122	0.167	0.004	0.240	**6.42×10^{-6}**	1.11×10^{-5}	0	1.93×10^{-5}	5.80×10^{-6}

Table 19. Cont.

	Biomass (t wet mass km^{-2})				Export (t km^{-2} yr^{-1})[a]				
Group	Value	± SD	Min	Max	Value	± SD	Min	Max	Est.
Arctic cod	0.021	0.027	0.002	0.052					
Large pelagics	0.033	0.012	0.020	0.043	**4.17 x 10^{-5}**	7.23 x 10^{-5}	0	1.25 x 10^{-4}	4.53 x 10^{-5}
Pisci. small pel. feeders	0.558	0.448	0.242	0.875	**2.95 x 10^{-2}**	8.80 x 10^{-3}	2.46 x 10^{-2}	3.66 x 10^{-2}	2.95 x 10^{-2}
Plank. small pel. feeders	1.630	0.240	1.413	1.888	**1.43 x 10^{-1}**	2.56 x 10^{-2}	1.22 x 10^{-1}	1.60 x 10^{-1}	1.46 x 10^{-1}
Shrimp	0.615	0.230	0.383	0.843	**1.26 x 10^{-1}**	4.81 x 10^{-2}	5.69 x 10^{-2}	1.74 x 10^{-1}	1.18 x 10^{-1}
Large crustaceans	0.862	0.204	0.369	2.142	**6.55 x 10^{-2}**	3.34 x 10^{-3}	6.04 x 10^{-2}	6.98 x 10^{-2}	6.55 x 10^{-2}
Echinoderms	112.300	55.904[b]							
Molluscs	42.100	20.958[b]			**2.83 x 10^{-2}**	6.19 x 10^{-3}	2.12 x 10^{-2}	3.23 x 10^{-2}	2.87 x 10^{-2}
Polychaetes	10.500	5.227[b]							
Other benthic invertebrates	7.800	3.883[b]							
Large zooplankton	9.643	14.482	0.010	63.000					
Small zooplankton	50.000	81.317	5.000	120.000					
Phytoplankton	23.411	16.474	5.009	45.452					
Detritus	132.608	113.440	61.630	222.058	5.94 x 10^{1}	0.59 x 10^{1}	**5.35 x 10^{1}**	**6.53 x 10^{1}**	5.35 x 10^{1}

[a]: Export was mainly the catch (including landings and anthropogenic mortality as hunting, etc.). For detritus, export was loss of detritus buried as sediment.

[b]: calculated as B_X*$CV(B_Y)_{mean}$ with $CV(B_Y)_{mean}$ = 66%, the average of all coefficients of variation for observed biomass.

[c]: calculated as Exp_X*$CV(Exp_Y)_{mean}$ with $CV(Exp_Y)_{mean}$ = 75%, the average of all coefficients of variation for observed export.

Table 20. Observed production and consumption used as input parameters for modelling for the 1994–1996 period in the northern Gulf of St. Lawrence. SD: standard deviation, Min: minimum, Max: maximum. Est: value estimates by inverse modelling. Values used in data equations or as upper and lower limit constraints are indicated in boldface. Means and SDs were calculated on the two extreme values.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Cetaceans	**0.016**	0.004	0.013	0.019	0.015	1.435	0.242	**1.264**	**1.606**	1.514
Harp seals	**0.010**	0.006	0.006	0.014	0.009	0.753	0.312	**0.532**	**0.974**	1.046
Hooded seals	**0.0005**	0.0002	0.0003	0.0006	0.0005	0.058	0.014	**0.048**	**0.068**	0.056
Grey seals	**0.0020**	0.0012	0.0011	0.0028	0.0018	0.132	0.091	**0.068**	**0.196**	0.183
Harbour seals	**0.0002**	0.0001	0.0002	0.0003	0.0002	0.020	0.006	**0.016**	**0.024**	0.024
Seabirds	**0.0011**	0.0008[a]			0.0012	0.309	0.280	**0.111**	**0.507**	0.153
Large cod	0.113	0.035	**0.075**	**0.208**	0.076	0.803	0.620	**0.365**	**1.242**	0.379
Small cod	0.020	0.016	**0.007**	**0.035**	0.059	0.336	0.420	**0.039**	**0.633**	0.238
Large Green. halibut	0.030	0.011	**0.024**	**0.040**	0.035	0.402	0.241	**0.231**	**0.572**	0.233
Small Green. halibut	0.107	0.072	**0.062**	**0.188**	0.096	0.866	0.738	**0.344**	**1.388**	0.412
Amer. plaice	0.203	0.065	**0.142**	**0.244**	0.220	3.046	2.945	**0.964**	**5.129**	1.059
Flounders	0.014	0.007	**0.009**	**0.020**	0.020	0.144	0.114	**0.064**	**0.225**	0.083
Skates	0.034	0.004	**0.030**	**0.039**	0.039	0.336	0.248	**0.161**	**0.511**	0.198
Redfish	0.190	0.147	**0.124**	**0.318**	0.250	9.288	11.110	**1.432**	**17.145**	1.484
Large demersals	0.024	0.004	**0.019**	**0.027**	0.040	0.390	0.303	**0.176**	**0.604**	0.257
Small demersals	0.060	0.073	**0.009**	**0.112**	0.092	1.083	1.190	**0.241**	**1.924**	0.402
Capelin	10.038	14.191	**0.076**	**481.700**	3.071	50.326	70.793	**0.267**	**100.384**	15.486
Sand lance	0.073	0.100	**0.002**	**0.144**	0.124	0.426	0.431	**0.122**	**0.731**	0.520

Table 20. Cont.

	Production (t km^{-2} yr^{-1})					Consumption (t km^{-2} yr^{-1})				
Group	Value	± SD	Min	Max	Est.	Value	± SD	Min	Max	Est.
Arctic cod	0.011	0.021	**0.001**	**0.031**	0.014	0.113	0.130	**0.021**	**0.205**	0.066
Large pelagics	0.005	0.002	**0.003**	**0.007**	0.009	0.194	0.228	**0.033**	**0.355**	0.042
Pisci. small pel. feeders	0.137	0.063	**0.080**	**0.200**	0.196	2.205	2.329	**0.558**	**3.852**	0.782
Plank. small pel. feeders	0.454	0.047	**0.403**	**0.499**	0.495	13.735	17.119	**1.630**	**25.840**	2.293
Shrimp	0.431	0.126	**0.323**	**0.596**	0.573	2.871	2.030	**1.435**	**4.306**	2.741
Large crustaceans	0.227	0.003	**0.217**	**0.237**	0.233	1.515	1.071	**0.757**	**2.272**	1.357
Echinoderms	33.667	38.755	**0.108**	**70.108**	32.920	243.147	185.156	**112.222**	**374.072**	119.850
Molluscs	22.949	34.282	**0.600**	**82.121**	69.072	165.744	126.214	**76.497**	**254.991**	237.726
Polychaetes	16.680	24.487	**0.206**	**74.564**	23.889	120.468	91.737	**55.601**	**185.336**	97.342
Other benthic invertebrates	9.173	7.631	**0.517**	**15.677**	7.738	66.252	50.451	**30.578**	**101.926**	46.723
Large zooplankton	26.578	9.661	**14.000**	**35.000**	23.602	156.076	155.147	**46.370**	**265.781**	118.426
Small zooplankton	232.943	159.725	**120.000**	**345.886**	282.899	996.401	789.507	**438.135**	**1554.666**	921.864
Phytoplankton	2185.476	1107.451	**1078.025**	**3292.927**	1129.019					
Detritus										

[a]: Calculated as P_X*$CV(P_Y)_{mean}$ with $CV(P_Y)_{mean}$ = 74%, the average of all coefficients of variation for observed production.

DISCUSSION

The CDEENA project is focussing on the comparison of different ecosystems (northern and southern Gulf of St. Lawrence, Newfoundland–Labrador Shelf, Scotian Shelf) for different time periods, i.e., the groundfish pre-collapse (1985–1987) and the post-collapse (1994–1996) periods. The time periods were determined after the analysis of biomass fluctuations for the key species of the northern Gulf system (i.e., cod and redfish) in the pre- and the post-collapse periods. These time periods have been chosen in order to have available and stable information on biomass (Jarre et al. 1991). The present data set was used to construct models of the northern Gulf of St. Lawrence for the post-collapse period.

The validity of any conclusion regarding the ecosystem being studied depends on the input data (and the confidence one has in them). The strengths and weaknesses of these inputs have to be judged. There are two levels of uncertainties in all mass-balance models. One level is which components (boxes and flows in the mass-balance models) to include in the starting configuration; the other level is the uncertainty of what the starting values should be for the minimum number of components that constrains the parameter estimation step.

Uncertainty in the input data

Ecosystem modelling requires the collection of a considerable amount of information. The modelling results described here were influenced by several areas of uncertainty for different groups at the lower and higher trophic levels. The quality of input data was variable. Catch estimates of commercial species are considered quite reliable although there is indirect but reliable evidence for non-negligible misreporting (non-reported landings and discards at sea) (Fréchet 1991; Hurtubise et al. 1992; Palmer and Sinclair 1997). Uncertainty also occurs for the catch estimate of small Greenland halibut, which was assumed to be null. However, this could be biased since there seemed to be a large by-catch of this species in the shrimp fishery in 1997–1999 (Orr et al. 2000) even though no information is available for the northern Gulf area. Good biomass estimates for harp and grey seal as well as harvested species are available, but abundance information on hooded seal and harbour seal biomass is limited, particularly for the mid-1990s. Likewise, the biomass of small cod in the area may be underestimated. A large proportion of small cod resides in the inshore and gradually moves offshore at ages of 1 to 3 years. Inshore areas are not covered as thoroughly and fishing techniques during research surveys are not adapted to assessing small cod abundance, particularly their winter distribution. Moreover, biomass data for forage species, benthic invertebrates, and zooplankton were sparse or non-existent for the area and period studied and were thus taken from the literature, or for the same area at other time periods. For fish, biomass estimates were calculated from sequential population analysis (cod and herring) or from scientific trawl surveys carried in the northern Gulf that were adjusted for catchability (Harley and Myers 2001).

Very little is known about fish and invertebrate production and consumption in the Gulf of St. Lawrence. For fish, the majority of production estimates were obtained assuming that production or total mortality is equivalent to biomass multiplied by natural mortality plus the catch in the absence of information on total mortality (P/B = Z) under the steady-state assumption. Unfortunately, we have few measures of natural mortality. In many cases we

assumed that natural mortality is equal to a fixed value to get a preliminary production estimate that can then vary over a wide range. It was also necessary to use empirical data from other areas and/or time frames (e.g., capelin, sand lance, arctic cod), or less specific information (e.g., pelagic feeders, benthic invertebrates) for production and consumption estimates.

Further uncertainties with diet data resulted from assuming that the diet of a key species is representative of the functional group to which it belonged, or attributing the proportion of "unidentified" in stomach content analyses in proportion to the different identified groups in the stomachs. The uncertainties remaining in the understanding of the ecosystem may come from incorrect values because no data exist, the confidence limits are too large or result from an inaccurate aggregation of species within one functional group, or from unknown mechanisms occurring in the ecosystem. Overall, even though the model is not a perfect representation of reality, it is probably as good as it can be with the information available.

Strengths and weaknesses of the modelling efforts

The synthesis of existing ecosystem information is designed to enable a whole-system view using parameters that are basic to understanding populations and the ecosystem (Okey and Pauly 1999). Compared to single-species models, multispecies mass-balance models improve our understanding of the dynamics of fish populations through a more realistic treatment of uncertainty and variability in population parameters (e.g., natural mortality) or by identifying additional non-target species and ecological linkages among species, either of which could be altered through fishing (Hollowed et al. 2000; Whipple et al. 2000). Among the multispecies models, inverse models are static-flow models that provide a "snapshot" of the system at one moment in time and use mass-balance principles and an objective least-squares criterion to estimate flows of organic matter or energy among components of an ecosystem. The use of upper and lower limits to constrain the majority of input values (production, consumption, and diet composition) and the choice of row and column weights make inverse modelling a flexible tool to quantify mass-balanced flow diagrams and trophic transfer efficiencies that are internally consistent.

However, due to the fact that our empirical databases and scientific understanding of ecological processes will always be incomplete (underdetermined system: the number of flows to be solved [$n = 470$ in this case] exceeds the number of independent mass balance relations [$m = 167$]), flow network solutions are not unique. Different approaches (comparisons of different flow networks, random perturbations, sensitivity tests) have to be used to allow for an explicit implementation and assessment of this uncertainty (or the solution's robustness) to variations in the data (Whipple et al. 2000). Indeed, mass-balance models estimate a very large number of parameters, and it is possible that the relatively limited data available are insufficient to constrain these parameters. Also, where one modelling approach compromises or simplifies portions of the system, another may provide a realistic and precise representation of the same parts of the system. In this study, by randomly perturbing data inputs, we constructed a set of balanced solutions and we used the mean of these 31 random perturbations. The estimated flows fall inside our a priori constraints (once the data are perturbed) and therefore are a reasonable "middle ground" description.

The model provides an overall view of the ecosystem, identifies general robust patterns, and shows where the uncertainties in the food web occur, that could be examined in future studies. Progress is still needed to refine our understanding of the structure of ecosystems in the Gulf of St. Lawrence as well as in other areas of the world.

CONCLUSION

This work is the result of a huge effort to assemble data on the biological characteristics of species occurring in the northern Gulf of St. Lawrence. Even though most of the data are good estimates for the 4RS ecosystem during the 1994–1996 period, some input values are rough estimates only, meaning that these values are assembled from different literature sources and not from independently measured parameters. Some errors in parameter estimates could significantly alter the system's biomass budget, especially for the most important species of the ecosystem, or produce a totally different balanced solution. Although the top predators appear to be reasonably represented, there is an evident lack of data on particular key species such as capelin, benthic invertebrates, and planktonic species. This illustrates the need for further work to improve the input parameters in order to enhance the quality of future modelling efforts. In conclusion, this model enabled us to bring together wide ranging data concerning the northern Gulf of St. Lawrence ecosystem. By doing so, it allowed us to focus attention on uncertainties in our knowledge on the ecosystem's structure and to identify where research efforts should be directed if we are to gain a better understanding of this ecosystem.

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See the CDEENA web site at http://www.osl.gc.ca/cdeena/en/accueil.shtml.

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